

FIGURE 17 - Hemimandibles (1, 2) and pelvis (3, 4) of *Equus altidens*, gnawed and fragmented by hyaenids. *Hémimandibules (1, 2) et pelvis (3, 4) d'Equus altidens rongés et fragmentés par des hyènes.*

assemblages (264 remains in Venta Micena, corresponding to 8 species ranging in body weight from 5 to 375 kg), which increases the randomness of their sampling (Wolf 1975; Palmqvist 1991, 1993; McKinney 1996). Secondly, the total number of skeletal remains (NISP) of each species is the best estimate of its abundance (A) in the assemblage, since

the counts of minimal number of individuals (MNI) tend to decrease the values of the common species and to overestimate those of rare species. Thirdly, analysis of only part of the assemblage is still valid, and species about which there is some uncertainty (such as would result from our inability to consistently identify their specimens) may be omitted

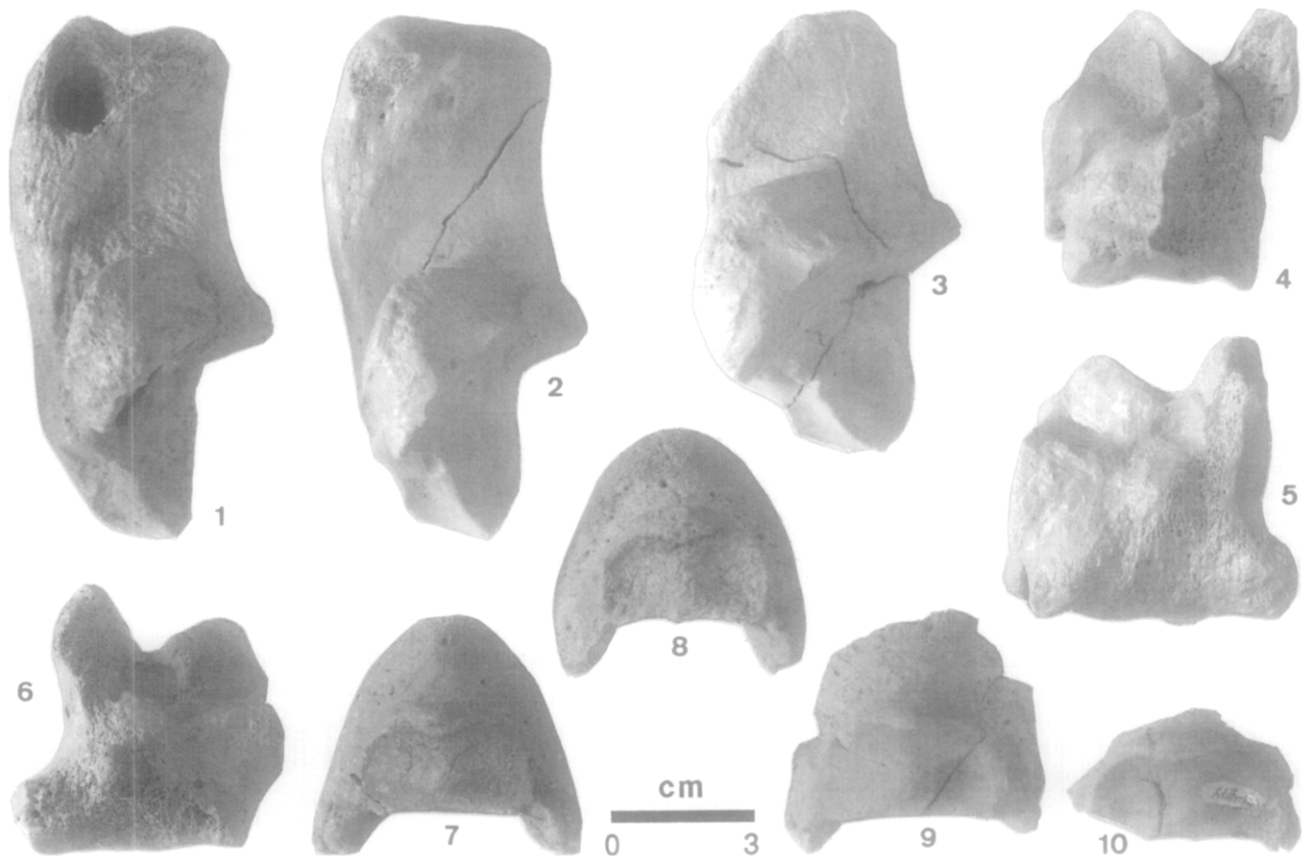


FIGURE 18 - Tarsal bones (calcanei [1-3] and astragali [4-6]) and third phalanges (7-10) of *Equus altidens*. One calcaneum shows marks made by insect larvae (1); two calcanei (2, 3), one astragalus (4) and one phalanx (9) have diagenetic fractures; one calcaneum (3), three astragali (4-6) and two phalanges (9-10) are partially gnawed by hyaenids. *Os tarsiens* (calcaneums [1-3], astragales [4-6]) et troisièmes phalanges (7-10) d'*Equus altidens*. Un calcaneum montre des marques faites par des larves d'insectes (1); deux calcaneums (2, 3), un astragale (4) et une phalange (9) ont des fractures diagenétiques; un calcaneum (3), trois astragales (4-6) et deux phalanges (9-10) sont partiellement rongés par des hyènes.

from the analysis with no loss of accuracy (Damuth 1982).

The values of $\text{Log}(A)$ and $\text{Log}(W)$ for the Venta Micena herbivore species ($N=9$) are shown in Figure 19A, in which the regression line obtained for both variates using for the adjustment the least squares method is also included. Two species were excluded from the analysis: *Praeovibos* sp., a mountain-dwelling species is poorly represented in the assemblage, given that it was clearly allochthonous to the palaeocommunity; Caprini indet. is represented by only one distal epiphysis of a metacarpal. The fit obtained in the adjustment is statistically significant at the 95% confidence level, but the slope is not included within the range of values anticipated by Damuth's model (-1.05 ± 0.25):

$$\text{Log}(A) = 9.448(\pm 1.626) - 0.598(\pm 0.253) \text{Log}(W); r = -0.665, F = 5.564 (p < 0.05).$$

In contrast, when we analyse the values for corrected abundance (A^*) of the species in the absen-

ce of taphonomic biases (Fig. 19B), the fit obtained is statistically significant at the 99.9% confidence level, and the slope is within the range of values predicted by the model:

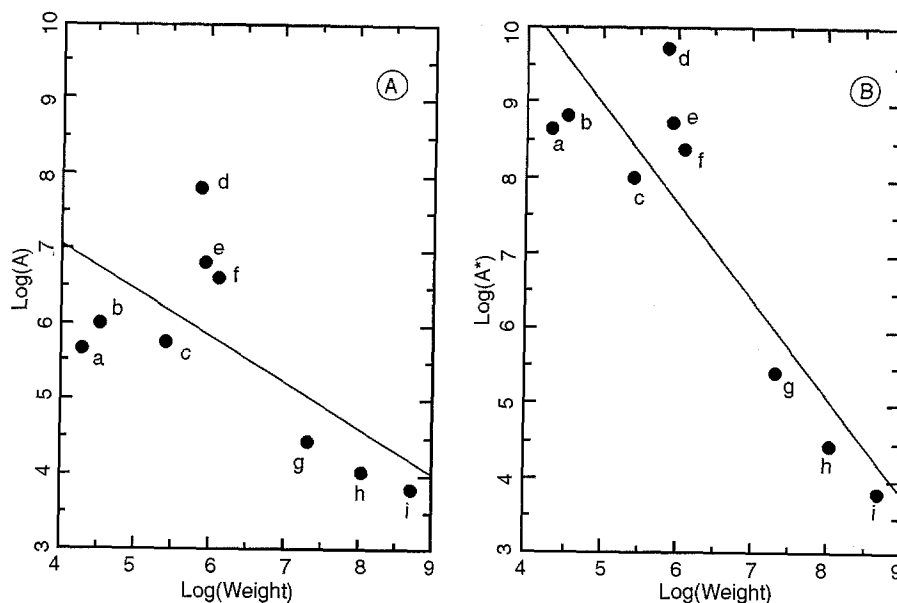
$$\text{Log}(A^*) = 15.367(\pm 1.626) - 1.278(\pm 0.253) \text{Log}(W); r = -0.885, F = 25.422 (p < 0.001)$$

These results confirm that the main loss of information during the taphonomic history of the Venta Micena assemblage was due to destruction of skeletal remains during the period when the bones were exposed on the surface before their definitive burial, and that the effects of this information loss were greater in species of smaller body size, thus biasing their quantitative representation in the fossil assemblage.

ABUNDANCE OF EPIPHYSES AND COMPLETE MAJOR LONG BONES

Two factors seem to have a substantial influence on the frequencies of skeletal parts in an untrans-

FIGURE 19 - Relationship between body weight (W, in kg) and abundance of skeletal remains (A: original abundance = NISP; A*, abundance corrected for taphonomic biases) in the ungulate species (N = 9) of the Venta Micena assemblage (A: regression line obtained for A vs. W, adjusted by minimum squares analysis; B, regression line for A* vs. W). a, *Hemitragus alba*, b, Cervidae gen. et sp. indet., c, *Soergelia minor*, d, *Equus altidens*, e, *Megaloceros (Megaceroides) solilhacus*, f, Bovini cf. *Dmanisibos*, g, *Stephanorhinus etruscus*, h, *Hippopotamus amphibius antiquus*, i, *Mammuthus meridionalis*. Relations entre le poids corporel (W en kg) et l'abondance des restes de squelettes (A: abondance originelle = NISP; A*, abondance corrigée des biais taphonomiques) pour les espèces d'ongulés (N = 9) de l'assemblage de Venta Micena (A: droite de régression obtenue pour A vs. W, ajustée par l'analyse des carrés minimaux; B, droite de régression pour A* vs. W).



ported assemblage (Binford 1978, 1981; Binford & Bertram 1977; Blumenshine & Madrigal 1993; Lyman 1984, 1994): structural density of bones and within-bone nutrient utility. Overall meat/bone utility plus ease of disarticulation are also important factors affecting skeletal part representation in accumulations transported by carnivores (see Lyman 1994, and references therein). Several taphonomic processes, such as carnivore damage (Marean & Spencer 1991), are mediated by the structural density of bones (mechanical and chemical attrition have greater effects on bones with low bulk density), and by the extraction of nutrients within bones, particularly marrow. Many structural density estimates, obtained using photon absorptiometry, are available in the literature (see Lyman 1994), but the estimation of within-bone nutrients is rather problematic. Interspecific differences in the distribution of flesh between the hindlimb and forelimb of bovids seem to be related to locomotor type (Blumenshine & Caro 1986). In a similar way, absolute long bone marrow yields differ among species, and among individuals of different size within a species. Most published data (Binford 1978; Blumenshine 1991; Emerson 1990; Jones & Metcalfe 1988) are clearly inadequate for assessing this variability. Only Blumenshine and Madrigal (1993) have addressed this issue, using a broad sample of East African ungulates.

Figure 20 shows the abundance of long bone epiphyses of ruminants in the Venta Micena assemblage and their mean bone mineral density (estimated from values obtained using photon absorptiometry in modern bison and deer; Lyman 1994). The positive relationship observed between both

variates is statistically significant, according with a least squares regression adjustment:

$$\text{Abundance} = -68.522(\pm 23.007) + 270.841(\pm 56.458) \text{Density}; r = 0.835, F = 23.01 (p < 0.001).$$

Similarly, Marean & Spencer (1991) found a strong correlation between the frequencies of long bone parts of domestic sheep that survived gnawing by spotted hyaenas and their structural density.

Figure 21 shows the abundance of major long bone epiphyses of ruminants and their mean fat content (estimated from values for moder bison in Brink 1997). The inverse relationship detected between both variates is also very significant, according with a least squares regression adjustment:

$$\text{Abundance} = 70.086(\pm 7.665) - 0.249(\pm 0.051) \text{Fat weight}; r = -0.839, F = 23.71 (p < 0.001).$$

However, the structural density of the bone is inversely related with its fat content, which is higher in those epiphyses in which the less denser, cancellous tissue predominate. Figure 22 shows a plot of density and fat content of epiphyses (x and y-axes), where the abundance of long bone epiphyses is represented by contour lines (z-axis) using 20 intervals of increasing value. A multiple regression approach to the estimation of epiphyses as a function of both their density and fat content has shown a statistically significant relationship:

$$\text{Abundance} = 0.706(\pm 59.438) + 138.176(\pm 117.883) \text{Density} - 0.137(\pm 0.108) \text{Fat weight}; r = 0.862, F = 13.002 (p < 0.002),$$

in which the fat content of the epiphyses is a somewhat better predictor of their abundance, as

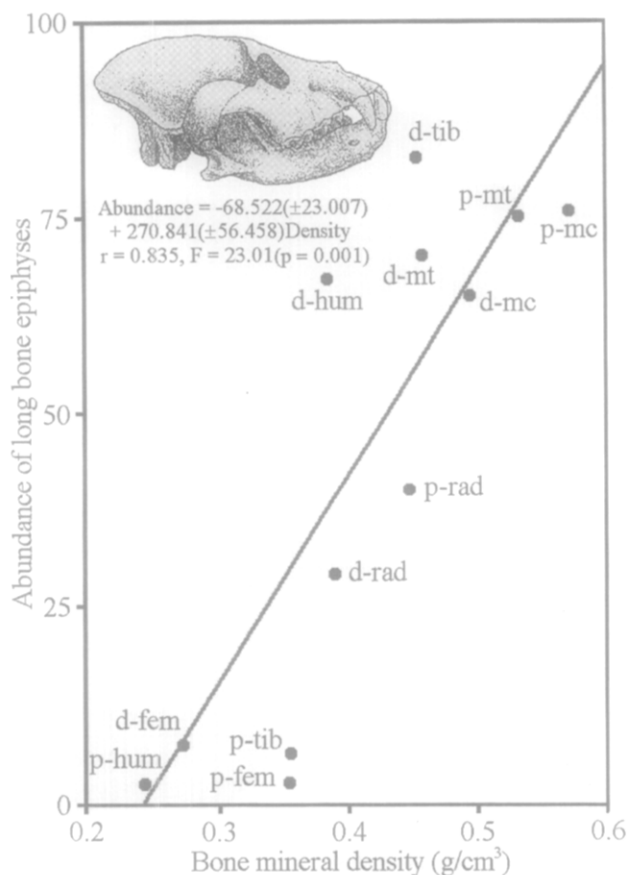


FIGURE 20 - Number of epiphyses (d: distal, p: proximal) of long bones (hum: humerus, rad: radius, mc: metacarpal, fem: femur, tib: tibia, mt: metatarsal) of ruminant species in the Venta Micena assemblage (data from Martínez-Navarro 1991) and mean bone mineral density (average of bison and deer; values obtained from Lyman 1994: Table 7.6). The regression line was adjusted by least squares analysis. *Nombre d'épiphyses (d: distales, p: proximales) d'os longs (hum: humérus, rad: radius, mc: métacarpien, fem: fémur, tib: tibia, mt: métatarsien) d'espèces de ruminants de l'assemblage de Venta Micena (données d'après Martínez-Navarro 1991) et moyenne de la densité minérale (moyenne de bison et de cerf; valeurs obtenues d'après Lyman 1994: Tableau 7.6). La droite de régression a été ajustée par l'analyse des moindres carrés.*

it may be deduced from the values of the standardized coefficients (0.428 and -0.460 for bone density and fat content, respectively). This is confirmed by the values obtained for the first order partial correlation coefficient of the abundance of epiphyses on their estimated structural density being constant their fat content ($r = 0.363$), and of the abundance of epiphyses on their fat weight with independence of their density ($r = -0.390$).

The abundance of major long bones of ruminants in Venta Micena (complete limb bones and long bone cylinders, lacking one or both epiphyses) and their mean wet weights of marrow content (esti-

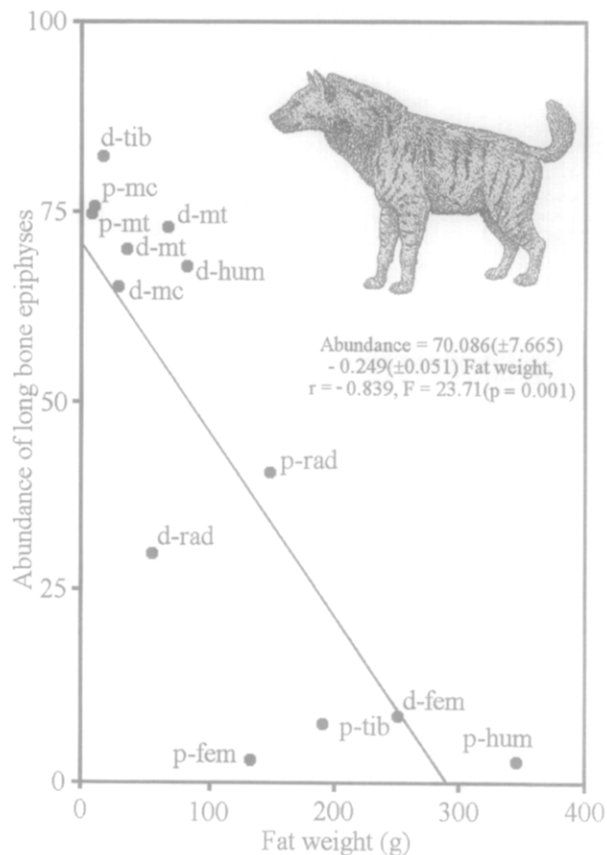


FIGURE 21 - Number of epiphyses (d: distal, p: proximal) of long bones (hum: humerus, rad: radius, mc: metacarpal, fem: femur, tib: tibia, mt: metatarsal) of ruminant species in the Venta Micena assemblage (data from Martínez-Navarro 1991) and mean bone fat content (estimated from modern bison in Brink 1997: Table 3). The regression line was adjusted by least squares analysis. *Reconstitution de Pachycrocuta brevirostris dessinée par Mauricio Antón (d'après Turner & Antón 1996). Nombre d'épiphyses (d: distales, p: proximales) d'os longs (hum: humérus, rad: radius, mc: métacarpien, fem: fémur, tib: tibia, mt: métatarsien) d'espèces de ruminants de l'assemblage de Venta Micena (données d'après Martínez-Navarro 1991) et moyenne du contenu gras des os (estimée d'après le bison moderne in Brink 1997, tabl. 3). La droite de régression a été ajustée par l'analyse des moindres carrés.*

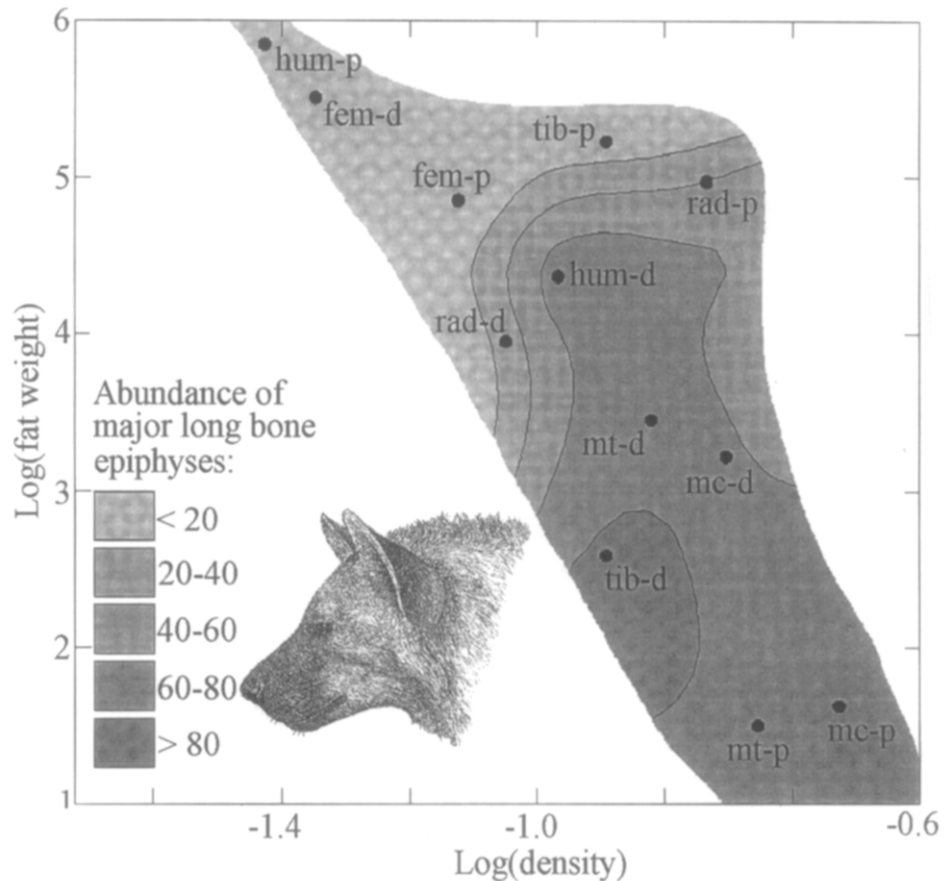
mated from values for modern wildebeest in Blumenschine & Madrigal 1993) is shown in Figure 23. There is an inverse relationship between the abundance of each long bone and its marrow content, which is linearized by means of logarithmic transformation as:

$$\text{Log}(\text{Abundance}) = 9.249(\pm 0.819) - 2.033(\pm 0.248) \text{Log}(\text{Marrow content});$$

$$r = -0.972, F = 67.29 (p < 0.001).$$

These results indicate the preferential consumption by hyaenas of low-density skeletal parts, dif-

FIGURE 22 - Density plot of abundance of long bone epiphyses (d: distal, p: proximal, hum: humerus, rad: radius, mc: metacarpal, fem: femur, tib: tibia, mt: metatarsal) represented by contour lines (z-axis) on mean structural density (x-axis) and fat content (y-axis). Reconstruction of the face of *Pachycrocuta brevirostris* drawn by Mauricio Antón (from Turner & Antón 1996). *Graphe de la densité de l'abondance d'épiphyses d'os longs (d: distales, p: proximales, hum: humérus, rad: radius, mc: métacarpiens, fem: fémur, tib: tibia, mt: métarprien) représentée par des lignes de contour (axe z) sur la moyenne de densité structurale (axe x) et le contenu gras (axe y). Reconstitution de la tête de Pachycrocuta brevirostris dessinée par Mauricio Antón (d'après Turner & Antón 1996).*



ferential fragmentation leading to less dense bone parts being crushed into unidentifiable fragments in contrast to denser bone parts simply broken into small but recognizable pieces during the extraction of marrow (Lyman 1994). The selective transport of certain anatomical parts and the preferential breakage by hyaenas of the richer marrow bones were thus major factors biasing the composition of the Venta Micena assemblage.

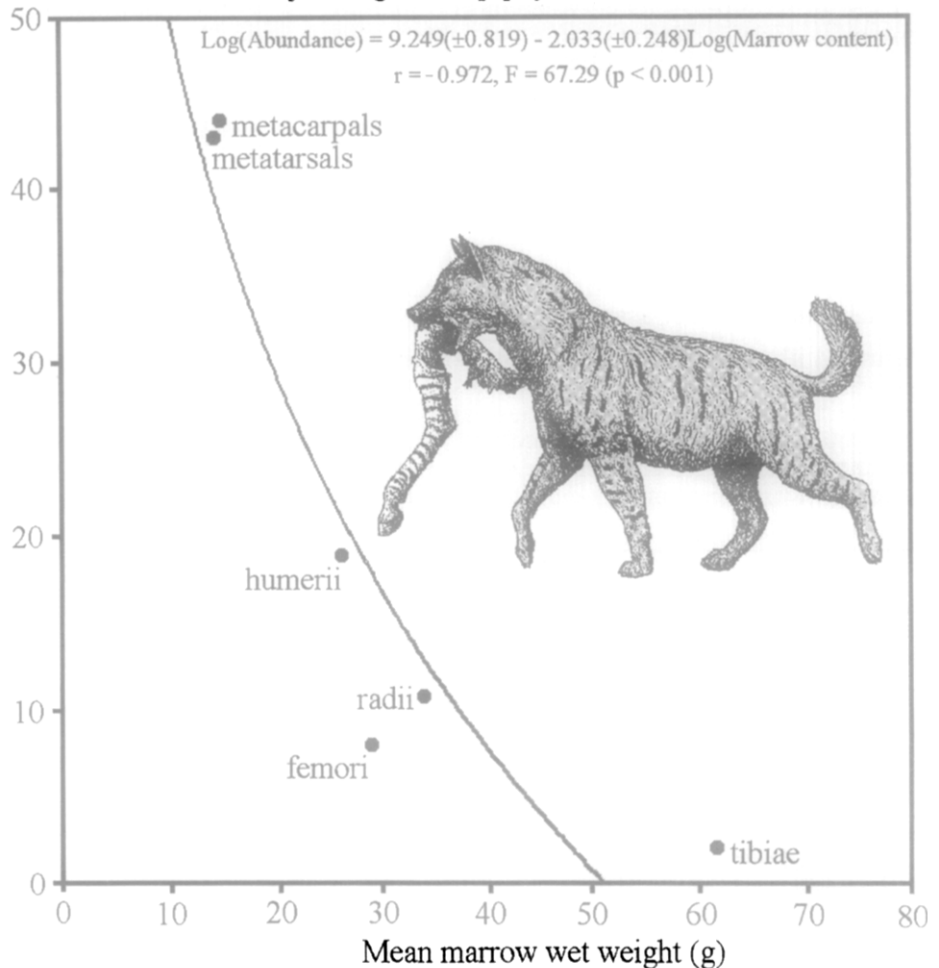
We can evaluate the extent of this taphonomic bias, which affected the original composition of the Venta Micena assemblage, by comparing the abundance of ruminants and equids which may be deduced from the number of complete metapodials, the most abundant major long bones preserved complete in the fossil assemblage, with the raw abundance of both groups of ungulates, which is easily estimated using MNI counts obtained from dental elements (Table 1). Ruminants are represented in Venta Micena by 87 metapodials, complete or long bone cylinders lacking only one epiphysis (44 metacarpals and 43 metatarsals), and equids by 136 metapodials (60 metacarpals and 76 metatarsals). The ratio of ruminants to equids is thus 0.640 (87/136, approximately 1 ruminant: 1.6 equids). However, ruminants are

represented in the assemblage by a higher MNI (111) than equids (70), with MNI estimated from teeth counts, and the ratio is therefore 1.586 (111/70, approximately 1 ruminant: 0.6 equids). Both estimations differ widely, but the latter is the most reliable of them, given that we expect no great differences in fossilization potential of teeth from ruminants and equids, while the preservation of complete long bones is highly biased by differential gnawing and fragmentation by hyaenas as a function of their structural density, fat and marrow content, as it was demonstrated before (Figs 20-23).

Total marrow yields of equid bones are on average five-fold smaller than those from ruminants (Blumenshine & Madrigal 1993): specifically, the mean weight of marrow content from the metapodials of Burchell's zebra is 6.22 g, while this estimate is of 14.23 g for wildebeest metapodials. The Venta Micena equid (*E. altidens*) was similar in size to modern *E. grevy*, with an estimated weight of approximately 350 kg (Palmqvist et al. 1996a). Given the fact that *E. burchelli* weighs on average 230 kg, we can estimate by simple linear interpolation a mean marrow content of 9.47 g for the metapodials of *E. altidens*. This means that one

FIGURE 23 - Number of major long bones (complete limb bones and long bone cylinders, lacking one or both epiphyses) of ruminant species in the Venta Micena assemblage (data from Martínez-Navarro 1991), and mean wet weights (in g) of marrow content (estimated from values for modern wildebeest in Blumenschine & Madrigal 1993; Table 2). The curve was adjusted by least squares analysis. Reconstruction of *Pachyrocuta brevirostris* drawn by Mauricio Antón (from Turner & Antón 1996). *Nombre d'os longs majeurs (os complets de membres et cylindres d'os longs sans l'une ou les deux épiphyses) d'espèces de ruminants de l'assemblage de Venta Micena (données d'après Martínez-Navarro 1991) et moyenne des poids frais (en g) du contenu de moelle (estimations d'après des valeurs pour le gnou in Blumenschine & Madrigal 1993, tableau 2). La courbe a été ajustée par l'analyse des moindres carrés. Reconstitution de Pachyrocuta brevirostris dessinée par Mauricio Antón (d'après Turner & Antón 1996).*

Raw abundance of major long bone epiphyses



metapodial of the Venta Micena equid had 1.503 times less marrow content than a metapodial of ruminant (the ruminant species identified in the assemblage range in body size from 8 kg for Caprini indet. to 450 kg for Bovini cf. *Dmanisibos*; the estimation of 14.23 g for the metapodials of modern wildebeest, a species with a body weight of 170 kg, is thus appropriate as an average for all ruminants preserved in the fossil assemblage).

Using the equation that relates the abundance of complete long bones with their marrow content [$\log(\text{abundance}) = 9.249 - 2.033 \log(\text{marrow weight})$] it is possible to predict that a decrease by a factor of 1.503 in the mean marrow content of a given long bone would translate in an increase by a factor of 2.290 of its abundance in the assemblage; in other words, if the mean marrow content of the ruminant metapodials would have been similar to that of the equid ones, the abundance of the former in the assemblage should be of approximately 199 complete elements, instead of 87. This figure gives a ratio of ruminants to equids of 1.463 (199/136,

approximately 1 ruminant: 0.7 equids), which is very close to that calculated from MNI counts (1 ruminant: 0.6 equids), and thus confirms that differential fragmentation by hyaenas was the major factor biasing the representation of ruminant postcranial bones in Venta Micena.

MULTIVARIATE ANALYSIS OF BONE FREQUENCIES

To determine the agents that were mainly responsible for the initial accumulation of bones at Venta Micena, we compared known frequencies of different types of postcranial bones in various fossil and recent assemblages (Table 2). This comparative data base includes bones exposed on the surface or partially buried in Amboseli National Park (Kenya), assemblages found at open feeding-places of several carnivore species, those from dens and lairs used by leopards, hyaenas and porcupines, and also the bones present in both recent human camps and archaeological assemblages. Bones were clustered in four groups (I: vertebrae;

II: ribs; III: limb and girdle bones; IV: phalanges) to facilitate comparisons between data from different bibliographic sources (many of which included complete lists, with the abundance of each skeletal element, but in several references the bones were already clustered in groups similar to those used here). The teeth, cranial elements and hemimandibles were excluded from the analysis, as their frequencies were highly variable (depending, for example, on whether hyaenas could or could not fracture the skulls), and such elements did not show any characteristic pattern that allowed discrimination of assemblages.

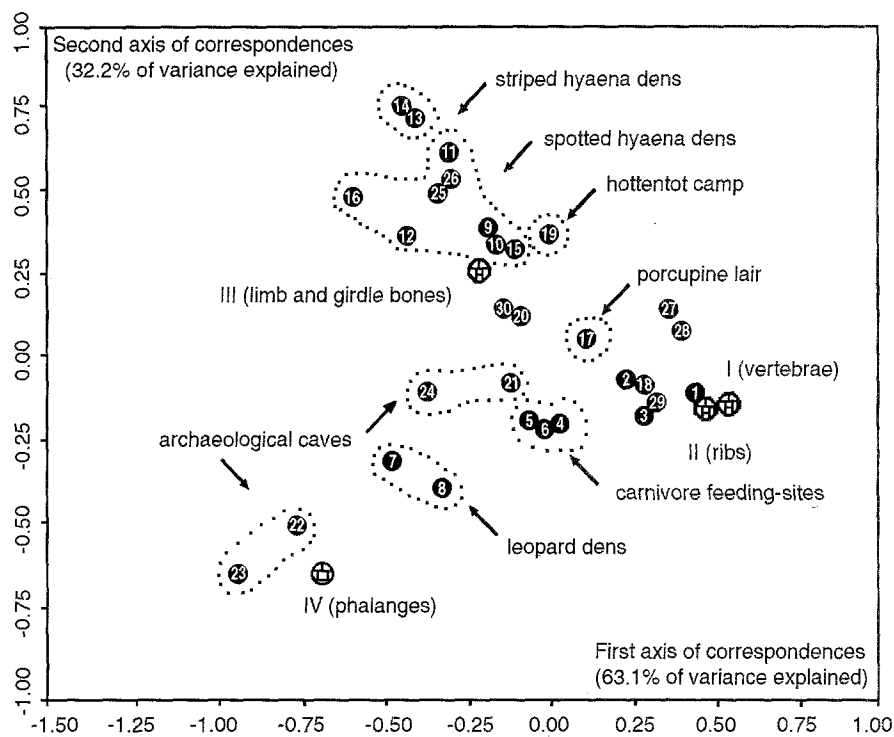
Figure 24 illustrates the results obtained in a correspondence analysis of the frequencies of the four types of bones (groups I-IV) in these assemblages. This multivariate statistical method was used because it is the most suitable for data on frequencies such as those in contingency tables (Reyment

& Jöreskog 1993). The two first correspondence axes explain more than 95% of the original variance. The assemblages we analysed show a parabolic or horseshoe distribution in the bivariate scatterplot for correspondence axes I and II (Guttman effect), which expresses a quadratic relationship between the latent vectors and indicates, among other things, a strong gradient in the frequencies of the different types of bones. The first factor is directly correlated with the abundance of vertebrae and ribs, the least persistent bony elements, with higher factor scores corresponding to assemblages in which these elements are predominant (bones exposed on the surface of Amboseli Park, in open carnivore feeding-places, in the porcupine lair and in the hunter-gatherer camp). This axis is inversely correlated with the frequencies of both phalanges and limb and girdle bones, elements that are more abundant in the remaining assemblages. The

Assemblages	I	II	III	IV	N	References
<i>Samples from modern ecosystems:</i>						
1 Bones exposed in Amboseli Park	35.7%	23.7%	34.8%	5.8%	13551	Behrensmeyer & Dechant-Boaz 1980
2 Bones buried 50% in Amboseli Park	32.9%	15.5%	42.1%	9.5%	624	Behrensmeyer & Dechant-Boaz 1980
<i>Carnivore feeding places:</i>						
3 Brown and spotted hyaenas	30.7%	23.3%	35.5%	10.5%	1080	Richardson 1980
4 Lions	24.2%	19.0%	39.8%	17.0%	483	Richardson 1980
5 Feral dogs	23.2%	17.2%	41.7%	17.9%	2334	Richardson 1980
6 Jackals	26.1%	15.6%	40.7%	17.6%	804	Richardson 1980
<i>Carnivore dens and rodent lairs:</i>						
7 Leopards	22.0%	0.0%	47.3%	30.7%	114	Brain 1981
8 Leopards	25.2%	4.9%	40.5%	29.4%	163	Brain 1981
9 Spotted hyaenas	12.9%	10.4%	70.3%	6.4%	202	Behrensmeyer & Dechant-Boaz, 1980
10 Spotted hyaenas	8.3%	15.8%	69.4%	6.5%	552	Bunn 1982
11 Spotted hyaenas	12.8%	0.9%	83.6%	2.7%	329	Brain 1981
12 Spotted hyaenas	10.7%	1.5%	76.2%	11.6%	206	Skinner et al. 1986
13 Striped hyaenas	7.0%	0.0%	90.8%	2.2%	357	Kerbis-Peterhans & Kolska-Horwitz 1992
14 Striped hyaenas	3.7%	0.7%	93.2%	2.4%	295	Skinner et al. 1980
15 Indet. hyaena den	21.2%	5.0%	67.5%	6.3%	80	Scott & Klein 1981
16 Upper Pleistocene hyaena den	2.6%	0.7%	84.5%	12.2%	2139	Klein & Cruz-Urbe 1984
17 Porcupines	35.9%	5.9%	49.9%	8.3%	726	Brain 1980
<i>Archaeological and modern human sites:</i>						
18 San hunter-gatherer camp	30.1%	19.8%	41.1%	9.0%	601	Bunn 1982
19 Hottentot camp (men and dogs)	9.3%	22.5%	65.4%	2.8%	755	Brain 1981
20 Middle Pleistocene level of Nazaret Cave	9.9%	21.6%	57.8%	10.7%	1616	Valensi 1991
21 Upper Pleistocene cave at Pomongwe	22.6%	10.6%	49.9%	16.9%	4082	Brain 1981
22 Upper Pleistocene cave at Booplaas	7.1%	5.3%	45.8%	41.8%	1408	Klein & Cruz-Urbe 1984
23 Upper Pleistocene cave at El Juyo	2.8%	4.1%	44.4%	48.7%	2324	Klein & Cruz-Urbe 1984
24 Neolithic cave at Fontbrégoua	12.7%	10.0%	54.7%	22.6%	885	Villa et al. 1986
<i>Pliocene and Lower Pleistocene sites:</i>						
25 Lower Pleistocene Site at Venta Micena	9.3%	5.0%	79.3%	6.4%	3208	Martínez-Navarro 1992a
26 FxJ20 level (main+east) at Koobi Fora	8.8%	6.4%	79.5%	5.3%	342	Bunn 1982
27 FxJ50 level at Koobi Fora	42.7%	8.8%	47.4%	1.1%	654	Bunn 1982
28 FLK Zinjanthropus Site level 22 at Olduvai	36.7%	17.4%	43.3%	2.6%	1900	Bunn 1982
29 FLK North level 6 at Olduvai	33.6%	21.4%	35.7%	9.3%	571	Bunn 1982
30 FKL North North level 2 at Olduvai	23.8%	6.0%	58.9%	11.3%	302	Bunn 1982

TABLE 2 - Relative frequencies of four types of postcranial bones (I: vertebrae; II: ribs; III: limb and girdle bones; IV: phalanges) in several fossil and recent assemblages. N: total number of bones in each assemblage. *Fréquences relatives de quatre types d'os postcrâniens (I: vertèbres; II: côtes; III: os des membres et des ceintures; IV: phalanges) de plusieurs assemblages fossiles et actuels. N: nombre total d'os dans chaque assemblage.*

FIGURE 24 - Results obtained in a factor correspondence analysis on the raw frequencies of different types of postcranial bones in several bony assemblages collected by carnivores, rodents and hominids (data from Table 2). The scatterplot of the factor loading values of the assemblages in the plane defined by the two first factor correspondence axes, which explain more than 95% of the original variance, follows a horse-shoe distribution (Guttman effect). The numbers of the assemblages refer to the numbers in Table 2. *Résultats obtenus par analyse factorielle des correspondances sur trois fréquences brutes de types différents d'os postcrâniens dans plusieurs assemblages d'os collectés par des carnivores, des rongeurs et des hominidés (données du Tableau 2). Le tracé dispersé des valeurs du facteur de charge des assemblages dans le plan défini par les premiers axes du facteur de correspondance, lesquelles expriment plus de 95% de la variance originelle, suit une distribution en fer à cheval (effet Guttman). Les nombres d'assemblages se rapportent aux nombres du Tableau 2.*



second factor shows higher projections for bone accumulations in which long bones are well represented, essentially those from spotted and striped hyaena dens, as well as those from the Hottentot camp (in which there are joint effects of *Homo* and *Canis* on bones), whereas negative values correspond to bone accumulations showing higher raw frequencies of phalanges (some assemblages accumulated by the man in caves from upper Pleistocene times, as well as from leopard dens).

The distribution of bone assemblages collected by the two main collecting agents (hominids and hyaenids) show quite different behavior: hyaenid accumulations are more homogeneous in composition (Table 2), since they consist mainly of group III skeletal elements (limb and girdle bones, excluding phalanges), whereas other types of bones are scarce in them. The greatest difference among the assemblages which were collected by hyaenas is found between dens of striped hyaenas (which are mainly carrion eaters due to their smaller size and solitary habits) and those of spotted hyaenas (whose larger size and strong social organization make them efficient hunters). In the former bone assemblages, ribs and vertebrae are almost absent, whereas in the latter ones these elements are somewhat more abundant, thus denoting less full utilization of the carrion. Contrariwise, the composition of bone assemblages due to anthropic action is more heterogeneous, and varies considerably depending on whether they derive from settlements established in an open camp or in a cave.

Venta Micena lies in the region of the factorial diagram occupied by the bone assemblages originating from spotted hyaena dens. With respect to the African Plio-Pleistocene assemblages analysed here, all with purported patterns of anthropic activity on bones (Bunn 1982), the level FxJj20 of Koobi Fora (main+east) is also included within the group of hyaenid-collected assemblages, close in position to Venta Micena, whereas level FxJj50 of Koobi Fora and Olduvai levels FLK 6 and 22 ("*Zinjanthropus*" site) are placed near the less-biased assemblages from open habitats. Olduvai level FLK North 2 takes an intermediate position between the two sets.

The results of the multivariate comparison suggest that the Venta Micena assemblage originated mainly through accumulation by hyaenas (*Pachycrocuta brevirostris*) at feeding places nearby their dens, of skeletal remains of the prey hunted by different carnivores. This interpretation is supported by analysis of the distribution of teeth and bones in the Venta Micena excavation quarry (Fig. 8), which shows two areas with greater abundance of skeletal remains, and which probably correspond to the bones dispersed at the entries of shallow dens, whose original structure was not preserved due to the sedimentary characteristics of the stratum and the diagenetic compaction. The recovery of relatively high numbers of deciduous teeth of *P. brevirostris* reinforces this hypothesis (as other carnivores are represented in the assemblage only by adult individuals) and helps to reject the possibility that bones

were accumulated in open feeding-places located at hunting sites distant from dens, since it can be presumed that infant individuals would not accompany adults on their hunts, but would stay near the dens, as occurs in modern spotted hyaenas (Kruuk 1972).

A MODEL OF PREY SELECTION

Four types of evidence strongly support a selection of prey by carnivores at Venta Micena during lower Pleistocene times (Palmqvist et al. 1996a): the interspecific analysis of the abundance of remains of juvenile individuals among ungulates, in relation to the average weight estimated for adults in each species; the U-shaped attritional mortality profiles deduced from crown height measurements in several ungulate species; the presence of many metapodials showing osteopathologies such as arthrosis, and; the sex ratio deduced from the metapodials of buffalos and equids, which is in both cases biased in favour of females.

JUVENILE/ADULT RATIOS

MNI counts for each species in the Venta Micena assemblage are shown in Table 1, in which the numbers of young individuals with deciduous teeth (from calfs to subadults or yearlings) and of adults with fully erupted permanent dentition are given. The percentage of juvenile individuals for each ungulate species, in relation to the mean weight estimated for adults, is shown in Figure 25. Larger species are represented in the fossil assemblage by a comparatively greater MNI of juveniles than those of smaller species.

The ratio of juvenile/adult individuals in a population depends on two factors: the annual birth rate or reproduction rate, and the duration of infancy. The reproduction rate scales approximately to the -0.3 power of adult body weight of a given species (the slope for births/year ranges from -0.26 [Eisenberg 1981] to -0.33 [Western 1979, 1980]). The duration of infancy is interspecifically related to body mass by a power close to 0.3 (0.29 for the time needed to reach reproductive maturity [Calder 1982, 1984] and 0.28 for the rate of incremental growth [Case 1978]). The proportion of juvenile individuals for a given species is thus the product of annual birthrate (B_i) and duration of infancy (D_i):

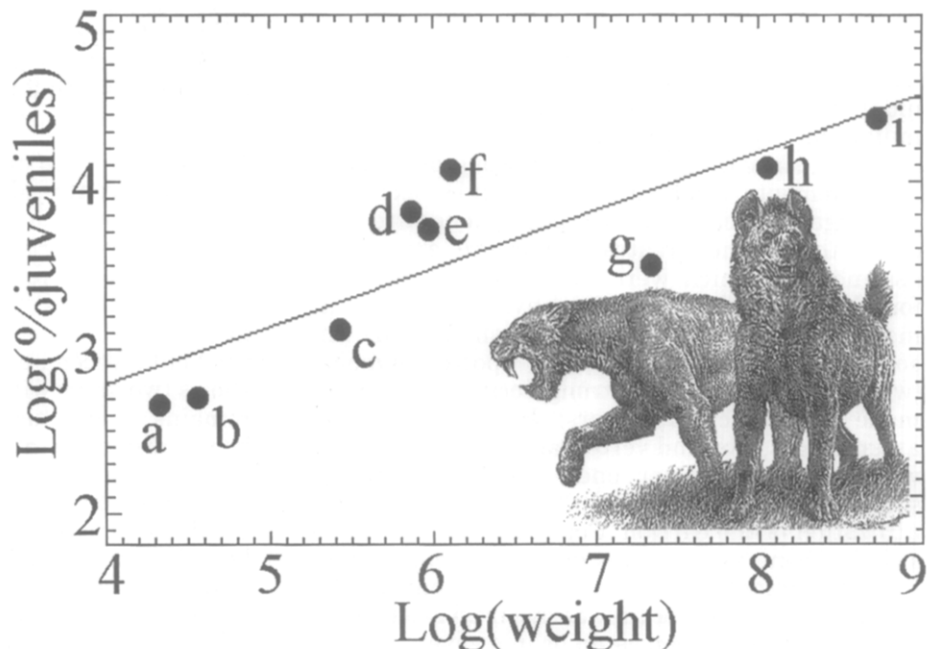
$$\% \text{juvenile individuals} = B_i D_i = K_1 W^{-0.3} K_2 W^{0.3} = K_3 W^0 = \text{constant.}$$

This percentage will be thus approximately constant and independent of species body size. However, in the ungulate species from the Venta Micena assemblage we noted a positive relationship between the two variates, which is highly significant statistically (Fig. 25):

$$\text{Log}(\% \text{ juveniles}) = 1.401(\pm 0.540) + 0.346(\pm 0.084) \text{Log}(W); r = 0.841, F = 16.95 (p < 0.004).$$

This result suggests strong selection by carnivores, according to the age and size of their ungulate prey, since predation of comparatively larger species such as elephant and hippo is focussed on juvenile and more vulnerable individuals, whereas in smaller species young and adult individuals are captured at similar frequencies.

FIGURE 25 - Least squares regression analysis of the proportion of juvenile individuals on estimated adult body weight (in kg) for ungulate species ($N = 9$) of the Venta Micena assemblage (data from Table 1): $\text{Log}(\% \text{ juveniles}) = 1.401 (\pm 0.540) + 0.346 (\pm 0.084) \text{Log}(\text{weight}); r = 0.841, F = 16.95 (p < 0.004)$. **a**, *Hemitragus alba*, **b**, Cervidae gen. et sp. indet., **c**, *Soergelia minor*, **d**, *Equus altidens*, **e**, *Megaloceros (Megaceroides) solilhacus*, **f**, Bovini cf. *Dmanisibos*, **g**, *Stephanorhinus etruscus*, **h**, *Hippopotamus amphibius antiquus*, **i**, *Mammuthus meridionalis*. Analyse de régression des moindres carrés de la proportion des individus juvéniles sur le poids corporel estimé (en kg) pour des espèces d'ongulés ($N = 9$) de l'assemblage de Venta Micena (données d'après le Tableau 1): $\text{Log}(\% \text{ de juvéniles}) = 1,401 (\pm 0,540) + 0,346 (\pm 0,084); \text{Log}(\text{poids}); r = 0,841, F = 16,95 (p < 0,004)$.



MORTALITY PROFILES

Interspecific analysis of juvenile/adult ratios for ungulates in Venta Micena indicates a different age of death depending on the size of the prey, as a consequence of selection by predators, which would increase the proportion of young and more vulnerable individuals hunted of those ungulate prey species of larger body size. However, the juvenile/adult ratios have poor resolution with respect to habitual prey age selection by carnivore species. Given this limitation, mortality profile patterns were deduced for those ungulate species which show greater relative abundance in the assemblage, the horse *Equus altidens* (MNI = 70, 37.4% of the total MNI of ungulates in the assemblage) and the large deer *Megaloceros (Megaceroides) solilhacus* (36, 19.3% of the ungulates). Age at death was calculated from dP_4 and P_4 crown height measurements (after Klein & Cruz-Urbe 1983, 1984).

The mortality curve deduced for *E. altidens* (Fig. 26A) indicates a clear U-shaped age profile, which suggests that death occurred mainly as a result of predation, and that predation was focussed both on very young individuals (most of them showing unworn dP_4) and past prime adults (with medium to heavily worn P_4). This pattern of mortality is similar to those observed for modern ungulate prey species hunted in a selective way by different carnivores ranging in size from the wild dog (*Lycaon pictus*) to the lion (*Panthera leo*) (Fig. 27).

The attritional profile of *M. solilhacus* (Fig. 26B) shows a very pronounced peak corresponding to death in the first 10% of potential lifespan. This difference with the mortality curve deduced for the horse may be due to the somewhat greater size estimated for the former species (269-568 kg, in contrast with a range of weights for *E. altidens* of 244-487 kg). The shape of the curve for *M. solilhacus* is similar to that found for Cape buffalo (*Syncerus caffer*) from the Middle Stone age layers of Klasies River Mouth Cave 1, South Africa (Klein & Cruz-Urbe 1983), which approximates an idealized attritional profile.

OSTEOPATHOLOGIES

A study of the long bones from Venta Micena have revealed many osteopathologies (Fig. 28A,B), the most frequent of which is arthrosis; it was found in the distal epiphysis of a metacarpal of a large deer (*M. solilhacus*) and in two third metatarsals of equid (*E. altidens*); both cases were manifested as considerable osseous overgrowths. Another type of abnormality was present in the diaphyses of a goat metacarpal (*H. alba*) and of an equid metatarsal, both of which present a wrinkled surface with osseous accretions. A third and more

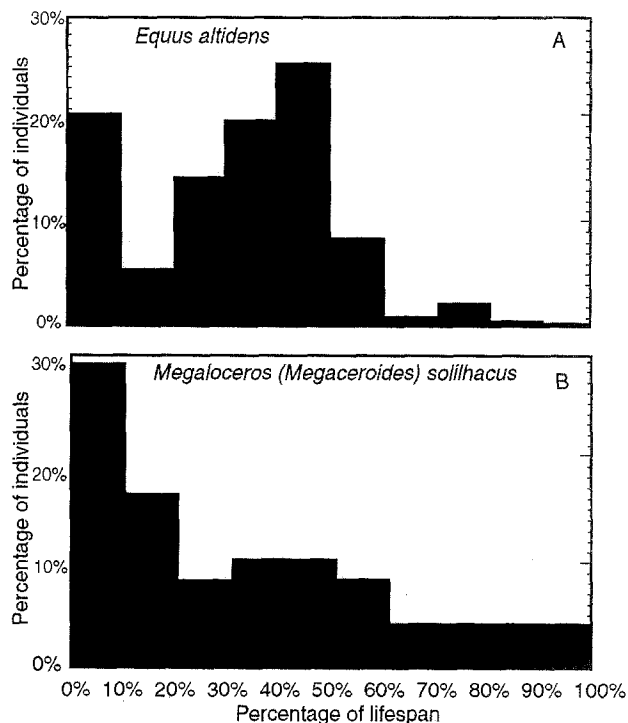


FIGURE 26 - Mortality profiles of *Equus altidens* and *Megaloceros (Megaceroides) solilhacus* in Venta Micena, calculated from dP_4 and P_4 crown height measurements (values for *E. altidens* kindly provided by V. Eisenmann, unpublished data, N = 81; values for *M. solilhacus* obtained from Menéndez 1987, N = 48). The proportion of death individuals in each 10% of potential lifespan interval was calculated using the software developed by Klein & Cruz-Urbe (1983). *Profils de la mortalité d'Equus altidens et Megaloceros (Megaceroides) solilhacus à Venta Micena, calculée d'après les mesures de la hauteur de la couronne de dP_4 et P_4 (valeurs pour *E. altidens* aimablement fournies par V. Eisenmann, données inédites, N = 81; valeurs pour *M. solilhacus* d'après Menéndez 1987, N = 48). La proportion d'individus morts pour chaque intervalle de 10% de la durée de vie a été calculée à l'aide du logiciel de Klein & Cruz-Urbe (1983).*

subtle type of osteopathology was found in the proximal epiphysis of several horse and buffalo (Bovini cf. *Dmanisibos*) metacarpals and metatarsals, affecting the articular facets of the metapodials, which were absent or showed abnormal growth. Results of a study of part of the Venta Micena collection indicate that these bone abnormalities are rather common: 13 out of 184 metapodials analysed of *M. solilhacus*, Bovini cf. *Dmanisibos* and *E. altidens* show signs of disease. Given that each ungulate has four metapodials, the pooled percentage of crippled animals of all three species would be approximately 28% (31% of equid, 19% of deer and 26% of buffalo). This proportion is higher than what would be expected in wild populations, and thus suggestive that such individuals in less than optimum condition were

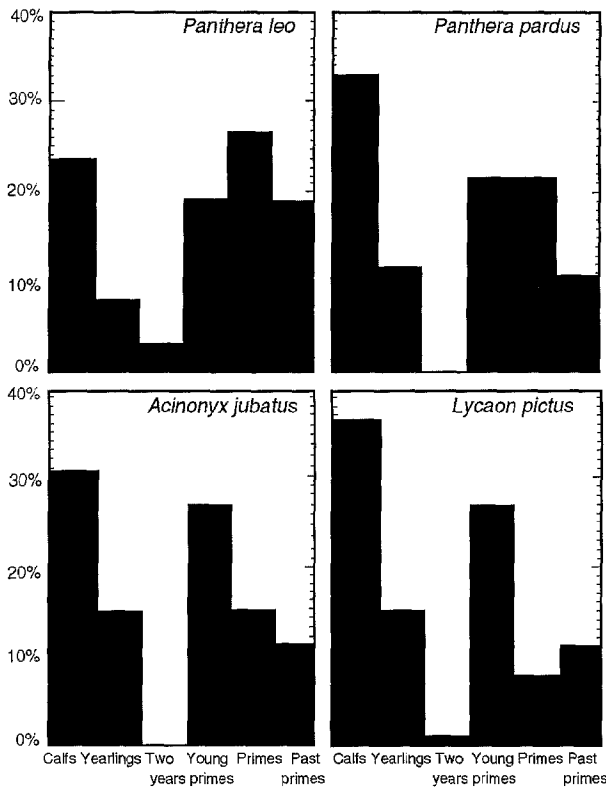


FIGURE 27 - Percentages of ungulate prey of different age groups (I: calfs, lambs, foals or piglets, less than 12 months old; II: yearlings; III: two years old animals; IV: young prime adults, with full permanent dentition but teeth having only light wear; V: prime adults, showing dentition with medium wear; VI: past prime adults with teeth showing heavy wear) hunted by large carnivores (*Panthera leo*, $N = 410$ kills; *Panthera pardus*, $N = 96$; *Acinonyx jubatus*, $N = 33$; *Lycaon pictus*, $N = 96$) in the Kafue National Park, Zambia (data for 20 ungulate prey species, Mitchell et al. 1965). Pourcentages des ongulés-proies dans des groupes de différents âges (I: veaux, agneaux, poulains et porcelets, âgés de moins de 12 mois; II: animaux d'un an; III: animaux âgés de deux ans; IV: jeunes adultes avec dentition permanente mais avec dents ayant seulement une légère usure; V: jeunes adultes avec une denture à usure moyenne; VI: adultes avec denture à usure importante) chassés par des grands carnivores (*Panthera leo*, $N = 410$ mises à mort; *Panthera pardus*, $N = 96$; *Acinonyx jubatus*, $N = 33$; *Lycaon pictus*, $N = 96$) dans le parc national de Kafue, Zambie (données pour 20 espèces d'ongulés-proies, Mitchell et al. 1965).

actively selected by the predators, since these pathologies must have limited the ability of the animals to run, thus reducing their chances of escaping from predators.

SEX RATIO IN UNGULATES

A third line of evidence of prey selection is provided by the analysis of sex ratio for the buffalo (Bovini cf. *Dmanisibos*), the largest ruminant of the Venta Micena assemblage. This bovid shows marked sexual dimorphism in the size of meta-

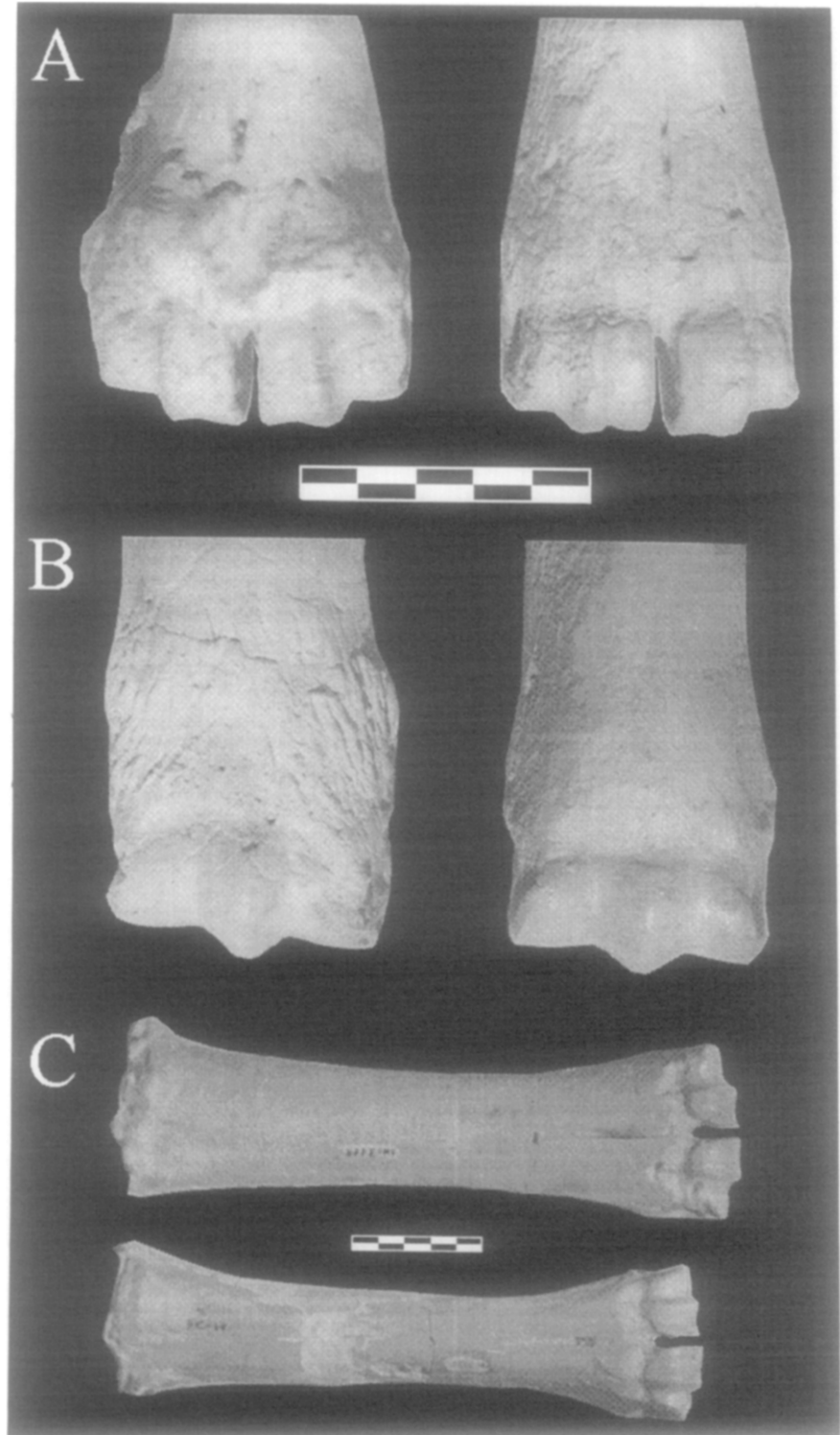
carpals (Fig. 28C), thus allowing estimation of the ratio of males and females in the fossil assemblage: 26% (5/19) and 74% (14/19), respectively (i.e., approximately 1: 3). These percentages are significantly different, according with a t-test ($t = 9.36$; $p < 0.001$), what suggests that predators selected female individuals, given their smaller body size.

The metapodials of the horse (*E. altidens*) do not show a clear bimodal pattern of size dimorphism as that exhibited by the buffalo, but linear discriminant functions developed using osteometric measurements allow to discriminate between the metapodials from males and females of *Equus grevyi*, the closest living analogue (both in size and shape) to the Venta Micena equid (Guerrero-Alba & Palmqvist 1998). When these functions are applied to the complete metapodials of the fossil species, 26% (11/42) of them are assigned to males (9 out of 24 metacarpals and 2 out of 18 metatarsals) and 74% (31/42) to females (15 out of 24 metacarpals and 16 out of 18 metatarsals), which are proportions remarkably similar to those found in the buffalo (i.e., 1 male: 3 females).

DISCUSSION

The stratigraphic and mineralogic data presented before allow us to propound the following sedimentary interpretation of the Venta Micena stratum: generation of a mudstone under a water sheet in a lacustrine environment (marginal facies); partial dessication of the palaeolake and subaerial exposure of the bottom, which preserves the previous microtopography; intense evapotranspiration and formation of an incipient calcrete paleosol (palaeorelief); development in the lowest topographic heights of ponds formed by micrite mud, which holded a small vegetational cover and experienced successive stages of dessication (rootmarks and mudcracks restricted to this zone of the stratum); and, finally, a new phase of massive generation of mudstone precipitated under water sheet conditions, what sealed the preexisting palaeorelief. The Venta Micena assemblage, in which all size intervals for bones and species of large mammals typical in a Pleistocene palaeo-community are represented, relies on this calcimorphic paleosol, whose irregular surface defined small trench like ponds and a surrounding area slightly more elevated, composed by a calcrete duricrust which formed the surface of a lacustrine margin. The substrate of these ponds was constituted by calcareous mud, which was dessicated at least three times, and includes the majority of the fossils which were preserved in the assemblage. There is no evidence of transport by water currents, since the bones show a random pattern in their orientation, there are no rounded or polished

FIGURE 28 - Osteopathologies in the epiphyses of metapodials (from Palmqvist et al. 1996a). **A**, arthrosis in a large deer (*M. solilhacus*) metacarpal (left: pathologic bone, right: healthy bone). **B**, arthrosis in an equid (*E. altidens*) metatarsal (left: pathologic bone, right: healthy bone). **C**, size dimorphism in buffalo (Bovini cf. *Dmanisibos*) metacarpals (above: male, below: female). *Ostéopathologies sur des épiphyses de métapodiaux (d'après Palmqvist et al. 1996a). A, arthrose d'un métacarpien de grand cerf (M. solilhacus) (à gauche: os pathologique, à droite: os sain). B, arthrose du métacarpien d'un équidé (E. altidens) (à gauche, os pathologique, à droite: os sain). C, dimorphisme de taille des métacarpies chez un buffle (Bovini cf. Dmanisibos) (en haut: mâle; en bas: femelle).*



edges, and detritics are nearly absent from the sediment.

The surface of the bones seems to have been exposed to the effects of insolation for a very short time interval, since only 10.7% of the palaeontolo-

gical sample shows incipient marks of subaerial weathering, with few shallow and small split line cracks due to insolation, and without mosaic cracking or exfoliation (weathering stage 1, Behrens-meyer 1978), what implies that the period of time

elapsed between the death of the individuals and the definitive burial of their skeletal remains was shorter than three years. The remaining 89.3% of the bones have no evidence of subaerial exposure (weathering stage 0, 0-1 year exposed before burial). These data, as well as the absence of sedimentary infilling in the bones which were preserved complete, indicate that the bones were buried with the periosteum intact and with fat content in their microstructure (i.e., they were buried when they were still in fresh condition).

THE COLLECTING AGENCY OF BONES

The elements from the estilopod, the zeugopod and the metapod predominate among the skeletal regions preserved, in many cases showing the original anatomical connections. The most abundant long bones are metapodials, tibiae, humeri and femori, of which only the metapodials are represented by a high percentage of complete elements. There are strong evidence which indicate that hyaenids were the biological agents responsible of the bone collecting and modifying processes, including the low number of isolated teeth and ribs, the prevalence of limb bones (of which the most abundant is the humerus in the forelimb and the tibia in the hindlimb), the high level of fragmentation of the bones (particularly proximal humeri with spiral fractures and distal tibiae with both spiral and longitudinal fractures), and the high number of gnawing marks made by premolars of large carnivores. All these features are typical of those bone assemblages collected by hyaenids (Skinner et al. 1980; Brain 1981; Horwith & Smith 1988). Additional evidence comes from the presence of many coprolites of large carnivores associated to the bones, and from the fact that *Pachycrocuta brevirostris* is the only carnivore species which is represented in the Venta Micena assemblage by relatively high numbers of both juvenile and adult individuals.

The bony assemblages accumulated by hyaenids are relatively homogeneous in their composition, since they are constituted basically by limb and girdle bones (excluding phalanges), while the remaining types of bones are poorly represented, because they were not collected or due to the selective destruction in the place where the skeletal elements were accumulated. Hyaenids were responsible at Venta Micena of at least four processes: selection and transport/collecting of bones; concentration; selection and alteration by the activity of adult individuals (splintering), and; selection and alteration by juvenile individuals (gnawing).

The main difference among bone assemblages collected by modern hyaenids is seen when we compare the dens of striped hyaenas (*Hyaena hyaena*)

and those of spotted hyaenas (*Crocuta crocuta*). Striped hyaenas are basically scavenger carnivores due to their small size and solitary habits, which use to transport to their dens parts of the carcasses of ungulates to feed the cubs (Mills 1989); ribs and vertebrae are nearly absent from these assemblages. Spotted hyaenas are efficient hunters, due to their greater size and strong social behaviour, and do not carry regularly carrion to their dens (Ewer 1973; Mills 1989); ribs and vertebrae are slightly more abundant in their assemblages, what may owe to a lower consumption of the bones, or to denote more interest for collecting these anatomical parts. Therefore, the type of preserved assemblage depends on the spatial context where the concentration and modification of the bones took place, and also on the behavior and age class of the bone collecting agency. The former considerations are supported on the differences between the dental pattern shown by both genera of modern hyaenids, because according to Bonifay (1971) the genus *Crocuta* shows less differenced cheek teeth, while the genus *Hyaena* presents more evolved dental features, which more closely resemble those of *Pachycrocuta*.

The bone assemblage preserved in Venta Micena would be generated by the selective accumulation of the skeletal remains from carcasses of ungulate prey hunted by different predators in the plains that surrounded the Pleistocene lake of Orce (predators: carnivores sensu lato; bone collecting agency: hyaenids), and by the alteration of the bones, also selective, made by both adult and juvenile hyaenids (bone modifying agency: *P. brevirostris*, the only eudemic carnivore in the assemblage), as it is usual in modern habitats (Sutcliffe 1970; Kruuk 1972; Brain 1981). The most abundant anatomical parts of the postcranial skeleton of ungulates which were preserved in the bone assemblage are the less nutritious, given their high mineral density and low fat content (for example, metapodials and distal fragments of humerus and tibia), while those bones with low structural density and high fat weight are represented by lower raw frequencies in the Venta Micena assemblage (for example, the distal epiphysis of femur, and the proximal epiphyses of both femur and tibia), because they were preferentially destroyed by hyaenas in order to extract the within bone nutrients.

All these data suggest that the activity of hyaenids took place in resting sites close to their dens. The finding of high numbers of deciduous teeth of *P. brevirostris* (unworn DP⁴ and germs of DP⁴) supports this hypothesis, and helps to reject the possibility that the skeletal remains were concentrated at hunting sites distant from the dens, since the young would not accompany adults on their

hunts, but would stay near the dens, as occurs in both modern spotted and striped hyaenas (Kruuk 1972; Mills 1989), in which juvenile individuals live in the dens until the age of 9-12 months (permanent dentition) or 12 weeks (deciduous dentition), respectively. The finding of only germs and unworn deciduous dentition implies that these teeth were not produced by tooth replacement, and it is thus a direct evidence of the death in situ of juveniles, what indicates that *P. brevirostris* had a similar behaviour to modern *Hyaena* and not to *Crocuta*. Such conclusion is also supported by the anatomy of the P_4 teeth in *Pachycrocuta*, which shows a *Hyaena* like structural pattern, opposed to that of *Crocuta*. This anatomical difference contrasts with the results of the bone modifying activity of *P. brevirostris*, which are analogue to those of fossil *Crocuta* in Europe.

The distribution of teeth and bones in the Venta Micena excavation quarry shows two areas with higher density of skeletal remains, which could correspond to the bones that were dispersed at the entry of the dens; the original structure of the dens, which were excavated by adult hyaenids in dry micrite mud, was not preserved due to the effects of diagenetic compaction. The model for Venta Micena may be analogous to one of the modern dens found in Amboseli National Park (Hill 1981).

The results obtained through applying Damuth's model to the interspecific analysis of the size/abundance patterns in ungulate species from the Venta Micena assemblage indicate that the main taphonomic bias was produced by differential collecting and fragmentation by hyaenids of skeletal remains during an interval of time prior to their definitive burial. These biostratigraphic agents biased the composition of the palaeocommunity according to the body sizes of the species it comprised, affecting bones of smaller species more markedly. However, the structure of the original palaeocommunity was partially preserved during fossilization, and it is possible to quantitatively estimate the original representation among the unrepresented fraction. This result is congruent with what is known concerning the origin of the Venta Micena assemblage (Gibert et al. 1992; Palmqvist et al. 1992; Mendoza et al. 1993), since all sedimentologic and taphonomic analyses indicate that bones were accumulated on a paleosol characterized by extensive emerged zones, among which were numerous shallow ponds, places where ungulates came to drink. In this muddy environment skeletal remains of the prey of carnivores were collected by the hyaenas around the entrance of dens dug near the ponds, where they were buried rapidly as can be deduced from the low rate of subaerial weathering.

The most likely hypothesis to explain the accumulation of bones in the assemblage is that in a period of desiccation of the ponds and fall of water level, hyaenas dug small, shallow dens which would then serve almost exclusively to protect their offspring from other carnivores and from the effects of insolation; adult individuals were probably safe from other predators given their large size and social behavior. The dismembered carcasses of animals that were eaten accumulated around the entries of dens. At some time the hyaenas abandoned their dens, probably as a consequence of a slight rise of the water level of the ponds, which caused the dens, dug in dry micritic mud, to be flooded and to collapse. Immediately thereafter the water level rose considerably, precipitating the micritic limestone and sealing the entire bone assemblage.

THE EVIDENCES FOR PREY SELECTION

The analysis of the juvenile/adult ratios of the ungulate species identified in the assemblage in relationship to the weights estimated for adult individuals suggests different mortality age profiles depending on the size of the prey, as a consequence of selection by predators, which would increase the proportion of young and more vulnerable individuals of the species of larger body size. This interpretation agrees well with available data on prey selection by recent carnivores as a function of size and age of the ungulate prey.

The mean percentages of juvenile individuals of each African ungulate species hunted, obtained by averaging the proportions of young killed by the five main predators (wild dog, cheetah, leopard, spotted hyaena and lion), are shown in Figure 29 (Table 3, data compiled from Palmqvist et al. 1996a). Percentages were calculated only for prey species with data available on the predation of juveniles by at least three species of carnivores, except for ungulate species of larger size (>1000 kg) which are only occasionally hunted by lions and spotted hyaenas. These pooled percentages would give the figures expected in an attritional assemblage originating exclusively from the accumulation of bones of hunted animals. A highly significant direct relationship exists between the percentages of young individuals and the body weights of the ungulate species:

$$\text{Log}(\% \text{ juveniles}) = 2.966(\pm 0.201) + 0.203(\pm 0.036) \text{Log}(W); r = 0.805, F = 31.38 (p < 0.0001).$$

The value for the slope in this fit (0.203) is within the 95% confidence interval of the slope that relates the percentages of juvenile individuals and the estimated weights for the ungulate species of Venta Micena (Fig. 25; slope = 0.346; standard error of slope = 0.084; confidence limits, with $p < 0.05 = 0.156 - 0.536$), and reveals that the two

parameters do not differ in a statistically significant way. Therefore, the proportions of juvenile individuals representing the ungulate species in the Venta Micena assemblage truly reflect prey selection by the carnivores as a function of body size of the prey hunted.

The increase in the value of the juvenile/adult ratios in relation with the weight estimated for the ungulate species allows us to rule out the hypothesis that the fossil assemblage was formed through catastrophic mortality events that would accompany recurrent droughts; in this case the percentage of juvenile individuals of the different species would be approximately constant and size-independent. We can consequently conclude that the immense majority of the skeletal remains accumulated by hyaenas in Venta Micena came

from attritional mortality in ungulate populations, caused by selective choice of carnivores.

The hypothesis of prey selection in the Venta Micena assemblage is also supported by the finding of various metapodials which show clear indications of osteopathology in the epiphyseal and diaphyseal regions, which would have affected the locomotive capabilities of the ungulates (Fig. 28A,B). In a study of the condition of prey, assessed from the state of the femoral marrow, Mitchell et al. (1965) found that 27% of ungulates killed by the lions, leopards, cheetahs and wild dogs were in fair or poor condition, as it may be deduced from the low quantities of fat content, while the remaining individuals preyed showed fat contents indicative of good condition. However, given the fact that the marrow test operates only at the lower end of the

Predators Prey ungulates	Wild dog, 25 kg (<i>Lycaon pictus</i>)	Cheetah, 50 kg (<i>Acinonyx jubatus</i>)	Leopard, 50 kg (<i>Panthera pardus</i>)	Spotted hyaena, 55 kg (<i>Crocuta crocuta</i>)	Lion, 160 kg (<i>Panthera leo</i>)
Thomson's gacelle, 23 kg (<i>Gazella thomsoni</i>)	30%	38%	20%	43%	39%
Springbok, 31 kg (<i>Antidorcas marsupialis</i>)	--	22%	27%	40%	27%
Reedbuck, 45 kg (<i>Redunca redunca</i>)	65%	--	60%	--	21%
Impala, 51 kg (<i>Aepyceros melampus</i>)	61%	34%	28%	--	41%
Grant's gacelle, 55 kg (<i>Gazella granti</i>)	50%	38%	38%	--	33%
Puku, 72 kg (<i>Kobus vardonii</i>)	--	33%	33%	--	
Warthog, 75 kg (<i>Phacocherus aethiopicus</i>)	--	--	87%	--	46%
Hartebeest, 150 kg (<i>Acelaphus buselaphus</i>)	64%	80%	86%	33%	32%
Gemsbok, 150 kg (<i>Oryx gazella</i>)	--	100%	100%	65%	35%
Wildebeest, 170 kg (<i>Connochaetes taurinus</i>)	83%	92%	93%	38%	27%
Waterbuck, 210 kg (<i>Kobus ellipsiprymnus</i>)	70%	100%	90%	--	28%
Burchell's zebra, 230 kg (<i>Equus burchelli</i>)	28%	100%	100%	42%	37%
Eland, 560 kg (<i>Taurotragus oryx</i>)	--	--	--	60%	16%
Buffalo, 600 kg (<i>Syncerus caffer</i>)	--	--	100%	--	23%
Giraffe, 1,100 kg (<i>Giraffa camelopardalis</i>)	--	--	--	87%	71%
Black rhino, 1,200 kg (<i>Diceros bicornis</i>)	--	--	--	90%	80%
Hippo, 2,000 kg (<i>Hippopotamus amphibius</i>)	--	--	--	100%	89%
White rhino, 2,500 kg (<i>Ceratotherium simum</i>)	--	--	--	--	100%
Elephant, 3,800 kg (<i>Loxodonta africana</i>)	--	--	--	100%	100%

TABLE 3 - Mean percentages of juvenile individuals of African ungulate species hunted by the five largest African predators (data compiled from Palmqvist et al. 1996a). *Moyennes des pourcentages des individus juvéniles d'espèces d'ongulés africains chassés par cinq grands prédateurs africains (données compilées d'après Palmqvist et al. 1996a).*

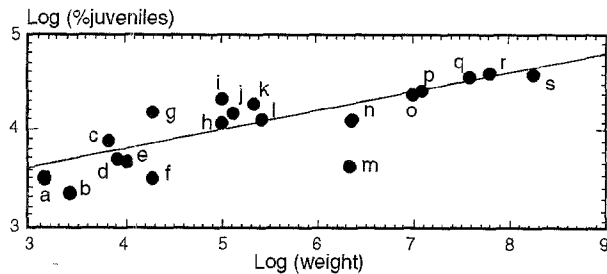


FIGURE 29 - Regression analysis by least squares method of the mean percentage of juvenile individuals (% juveniles) of several African ungulate species (N = 19) hunted by the five large African predators (*Lycaon pictus*, *Acinonyx jubatus*, *Panthera pardus*, *Crocuta crocuta* and *Panthera leo*) on mean adult body weight (in kg): $\text{Log}(\% \text{ juveniles}) = 2.966(\pm 0.201) + 0.203(\pm 0.036) \text{Log}(\text{weight})$; $r = 0.805$, $F = 31.38$ ($p < 0.0001$). a, *Gazella thomsoni*, b, *Antidorcas marsupialis*, c, *Redunca redunca*, d, *Aepyceros melampus*, e, *Gazella granti*, f, *Kobus vardonii*, g, *Phacochoerus aethiopicus*, h, *Alcelaphus buselaphus*, i, *Oryx gazella*, j, *Connochaetes taurinus*, k, *Kobus ellipsiprymnus*, l, *Equus burchelli*, m, *Taurotragus oryx*, n, *Syncerus caffer*, o, *Giraffa camelopardalis*, p, *Diceros bicornis*, q, *Hippopotamus amphibius*, r, *Ceratotherium simum*, s, *Loxodonta africana*. Data calculated from Table 3. Analyse de régression par la méthode des moindres carrés du pourcentage moyen des individus juvéniles (% juveniles) de plusieurs espèces d'ongulés africains (N = 19) chassés par les cinq grands prédateurs africains (*Lycaon pictus*, *Acinonyx jubatus*, *Panthera pardus*, *Crocuta crocuta* et *Panthera leo*) sur la moyenne du poids corporel adulte (en kg): $\text{Log}(\% \text{ juveniles}) = 2,966 (\pm 0,201) + 0,203 (\pm 0,036) \text{Log}(\text{poids})$; $r = 0,805$, $F = 31,38$ ($p < 0,0001$).

condition scale, the proportion of unhealthy individuals preyed upon by these predators is probably underestimated. The selection of prey in poor condition is higher for those ungulate species of larger body size: 68.4% of buffalo killed by lions, in contrast with only 9.1% of hartebeest, 8.5% of wildebeest, and 23.5% of zebra (Mitchell et al. 1965; Schaller 1972). Similarly, Crisler (1956) found that the caribou the wolf catches is usually the one that slows down: at least 50% of the kills involve crippled or sick individuals, whose incidence is 1.8% or even lower in the caribou herds.

THE HUNTERS AND THEIR PREY AT VENTA MICENA

It is always difficult to determine the role played by different carnivores in a palaeocommunity. Evidence that supports the model of prey selection proposed here (the results of the interspecific analysis of juvenile/adult ratios in ungulate species, the U-shaped mortality profiles, the presence of many bone diseases, and a biased intersexual ratio of large bovids and equids) clearly indicates that most of the skeletal remains preserved in the Venta Micena assemblage come from hunted individuals. But, who were the hunters?

Four large carnivore species have been preserved in the assemblage: the great saber-tooth *Homo-*

therium latidens, the medium-sized saber-tooth *Megantereon whitei*, the large hyaena *Pachycrocuta brevirostris* and the wild dog *Canis (Xenocyon) falconeri*.

Saber-toothed cats, which belong to the subfamily Machairodontinae, share among others the following craneodontal derived characters (see for review and references Biknevicius et al. 1996; Emerson & Radinsky 1980; Marean 1989; Van Valkenburgh & Ruff 1987):

- Elongate and flattened upper canines of two basic types: *Homotherium* (tribe Homotherine) had scimitar-shaped canines relatively short and broad, which were serrated bearing coarse crenulations, while *Megantereon* (tribe Smilodontini) showed dirk-shaped canines, extremely long, narrow, and without serrations.

- Enlarged upper incisors, which are relatively longer, thicker, more pointed and procumbent than in modern felids, and reduced, incisor-shaped lower canines. The incisor row is long and strongly curved, what suggests for saber-tooths a functional emphasis on these teeth for tearing and stripping flesh from carcasses, a task that modern felids perform with the assistance of their stout and conical shaped canines; the extremely large upper canines of the saber-tooths would probably be ineffective at the manipulation of chunks of flesh.

- Upper carnassials (P^4) with a reduced or absent protocone (lingual lobe), which is lowered away from the occlusal surface in *Megantereon*, thus removing it from its role as a hammer for bone crushing (a condition that is only present among extant felids in the hypercarnivorous cheetah), and is lost in *Homotherium*, in which there is also an anteriorly added accessory cusp. This teeth forms in saber-tooths a long thin blade, which is extremely specialized for slicing flesh, and allowed them to deflesh their prey rapidly.

- A lowered glenoid fossa, a reduced height of the coronoid process, a laterally shifted angular process, and a shortened zygomatic arch. All these features allow a wider gape than that of modern felids, but suggest that the temporalis muscle was weaker. However, the temporal fossae was shorter and narrower, which indicates that the temporalis was oriented in saber-tooths more vertically and perpendicular to the tooth row than in modern felids. This increased the bite force at the carnassial (M_1), which was closer to the mandibular condyle, although it remained significantly lower than in felids.

- An enlarged, lowered and ventrally extended mastoid process, which is enormous relative to modern felids, what indicates that the cleido- and sterno-mastoid muscles must have been corres-

prisingly large. The occiput is in most saber-tooths relatively higher and narrower than in felids, and the temporomandibular joint is located more ventrally. The mastoid process is rotated further below the skull joint so that the leverage of the neck muscle is increased, thus suggesting that a head-depressing motion was involved in the penetration of the canines.

The postcranial skeletons of scimitar-toothed and dirk-toothed machairodonts are quite different. *Homotherium* was a relatively long legged pursuit predator with the size of a modern lion, which had a comparatively large brain with an enlargement of the optic centre, a condition similar to that of the cheetah (Rawn-Schatzinger 1992). The morphology of *Homotherium* is unique among extant and past felids, showing relative limb proportions which indicate increased cursoriality and less prey grappling capabilities than other saber-tooths. The brachial index (i.e., radius length/humerus length) takes values close to or above 100%, what implies that most species of this genus preferred open habitats (Lewis 1997). *Megantereon* was a relatively short limbed ambush hunter, with a comparatively smaller brain, showing olfactory lobes well developed. It had powerfully developed forelimbs, what suggests that a killing bite in the throat may have been coupled with the immobilization of the prey by the front limbs. Comparative multivariate analysis of postcranial measurements (Lewis 1997) indicates for *Megantereon* an overall morphology similar to that of extant jaguars, with tree catching and long distance dragging capabilities; the low value for the brachial index suggests closed habitat preferences. As it will be discussed in detail below, morphofunctional studies currently in progress of African *M. whitei* from Venta Micena indicate that this predator generated large amounts of carrion, since it would exploit the carcasses of its prey to a small degree.

All these features indicate; that saber-toothed felids were able to hunt very large prey relative to their own size, and; that they left on the carcasses of the ungulates hunted large amounts of flesh and all within bone nutrients, which were available to be subsequently scavenged by hyaenids and hominids (Marean 1989). Sabertooths became extinct in East Africa by 1.5 Ma ago, what coincides with the emergence of the Acheulean Industrial Complex, but inhabited Eurasia until 0.5 Ma (Turner 1990, 1992). Their persistence may then explain the success of both *P. brevirostris* and hominids with Oldowan technology in Eurasia, where the Oldowan/Acheulean transition took place much later than in Africa, at approximately 0.5 Ma (i.e., when saber-tooths disappeared in this continent), since the Oldowan

sharp flakes were fully appropriate to scavenge on carcasses partially defleshed by saber-tooths and the cores were used by hominids in breaking bones for their marrow content.

C. falconeri was a hypercarnivorous canid widely distributed during the late Pliocene and early Pleistocene in the Old World (Rook 1994). This species had a large body size, comparable with that of the living northern races of *Canis lupus*, and was characterized by a relatively short neural cranium and a narrow muzzle. The sagittal crest is strong and the bullae are inflated. Features of the dentition include M_2 with a relatively reduced metaconid, and M_1 with a stoutly built talonid, consisting of a preeminent hypoconid relative to the entoconid, and a reduced metaconid. The lower premolars usually show accessory cusplets, and the mandibular ramus is high and heavy. The upper molars, and specially the upper carnassials, show a marked tendency to ward brachydonty; a wide occlusal basin is present at the base of the metacone and paracone in the M^1 , and the M^2 is large. The metacarpal II has a very reduced articular facet for the metacarpal I, what indicates that the latter bone was vestigial if not absent, a condition similar to that of *Lycaon pictus*, the only extant canid with a tetradactyl forelimb (Rook 1994).

P. brevirostris was an African giant, short-faced hyaena relatively common in lower Pleistocene European assemblages of large mammals (Howell & Petter 1980). It had a body and skull 10-20% larger than the modern spotted hyaena, *Crocuta crocuta*, and thus probably had greater ability than the latter species for destroying carcasses and consuming bone (Turner & Antón 1996). In Europe, *P. brevirostris* is first recorded in lower Pleistocene deposits at Olivola, and its last appearance is in the early middle Pleistocene site at Süssenborn. This species differed from other hyaenids in having a relative shortening of the distal limb segments, as reflected in the ratio of radius length to humerus length (88%; modern hyaenids range between 99% for the brown hyaena, *Parahyaena brunnea*, and 106% for the striped hyaena, *Hyaena hyaena*) and in the ratio of femur length to tibia length (74%; values of modern species range from 80% in *C. crocuta* to 89% in *H. hyaena*). These differences suggest a less cursorial life style for *P. brevirostris*, although such shortening could provide greater power and more stability to dismember and carry large pieces of carcasses obtained from aggressive scavenging (Turner & Antón 1996).

P. brevirostris was replaced in Europe by *Pliocrocuta perrieri* according with Turner (1992) and Turner & Antón (1996), but in Spain there is

no Pleistocene record of the latter species and *P. brevirostris* is substituted directly by *C. crocuta*. However, the finding of *P. perrieri* in French sites of middle Pleistocene age like Lunel Viel can be also explained by reworking of Pliocene fossils of this species, as occurs in the Spanish karstic site at Cueva Victoria. As discussed before, the extinction in Europe of *P. brevirostris* seems to have been linked to the decline and subsequent disappearance of machairodonts, particularly *M. whitei*, what implied the loss of an important source of partly-consumed carcasses, and thus a change in the interactions between flesh-eating and bone-cracking species of the carnivore guild (Martínez-Navarro & Palmqvist 1996; Turner & Antón 1996).

A possible way to deduce the respective ecological roles of the fossil carnivores preserved in the Venta Micena palaeocommunity may be to compare their hunting behavior with those of their modern analogs. Figure 30 shows the mean percentages of ungulates of different size classes (<50 kg, 50-150 kg, 150-400 kg, 400-800 kg, and >800 kg) that are killed and scavenged by the five main African predators (lion, spotted hyaena, cheetah, leopard and wild dog) (data compiled in Palmqvist et al. 1996a). As can be appreciated, lions and spotted hyaenas show similar hunting preferences according to prey body size: most kills involve animals that weigh between 50 and 150 kg. However, lions capture more ungulates of 150-400 kg, and especially of more than 400 kg, while hyaenas prey more often on smaller species (<50 kg). Cheetahs and leopards show similar hunting behaviors, killing mostly ungulates of less than 50

kg. Prey of wild dogs show two peaks: ungulates of less than 50 kg, mostly Thomson's gazelle, and animals weighing between 150 and 400 kg, like the wildebeest, which they are able to capture thanks to their cooperative hunting techniques. When these graphs are compared with that for the Venta Micena assemblage (Fig. 31), some interesting similarities emerge: the maximum for Venta Micena is in the intermediate size category (150-400 kg), similarly to the prey hunted by the lion and the wild dog, and there are two minima for the highest and lowest weight classes. The abundance in the fossil assemblage of large ungulates (>400 kg) is similar to the proportion of such prey species in lion kills. The relative scarcity of ungulates weighing less than 150 kg in comparison with the abundance of skeletal remains from species of 150-400 kg resembles the proportion of captures by wild dogs. These results suggest that two carnivores -the lion-sized saber-toothed felid *H. latidens* and the canid *C. falconeri*- played important ecological roles at Venta Micena.

However, one question remains: what was the role of the large hyaenid *P. brevirostris* in this palaeocommunity? Modern spotted hyaenas both kill and scavenge ungulates, depending on factors such as their interaction with lions and other predators (see Kruuk 1972). The remarkably similarity between the mean percentages of ungulates of the five size classes that are scavenged by modern spotted hyaenas (Fig. 30, data from Henschell & Skinner 1990; Kruuk 1972) and the abundance of these size categories in the fossil assemblage clearly indicates that *P. brevirostris* fed largely on ungulates preyed upon by other predators. The only differen-

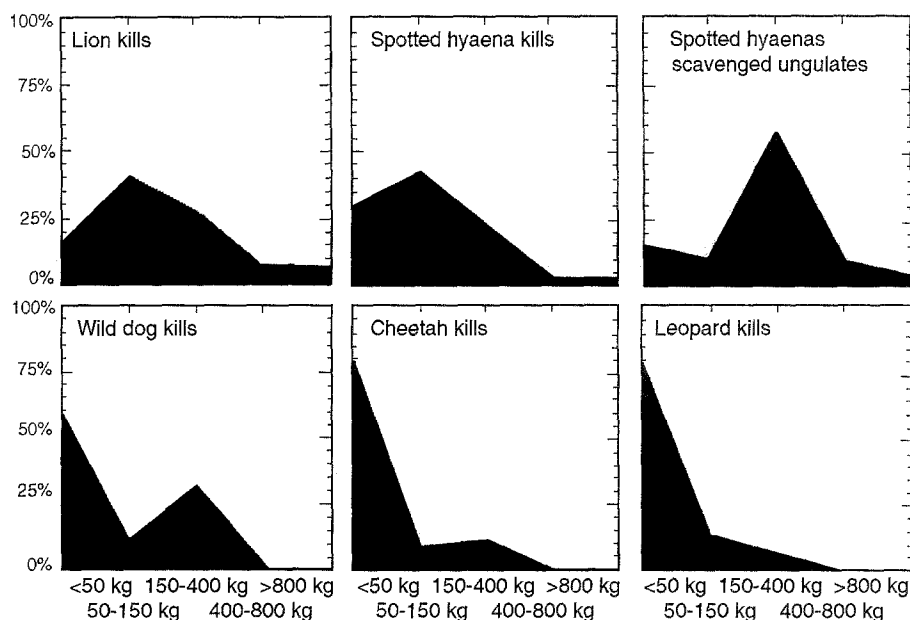


FIGURE 30 - Mean percentages of several ungulate size classes (a: <50 kg, b: 50-150 kg, c: 150-400 kg, d: 400-800 kg, e: >800 kg) killed and scavenged by the five main African predators (lion, spotted hyaena, cheetah, leopard and wild dog; data from Palmqvist et al. 1996a). Pourcentage des moyennes des classes de taille de plusieurs ongulés (a: < 50 kg, b: 50-150 kg, c: 150-400 kg, d: 400-800 kg, e: >800 kg) tués et dévorés par les cinq principaux prédateurs africains (lion, hyène tachetée, guépard, léopard et chien sauvage; données d'après Palmqvist et al. 1996a).

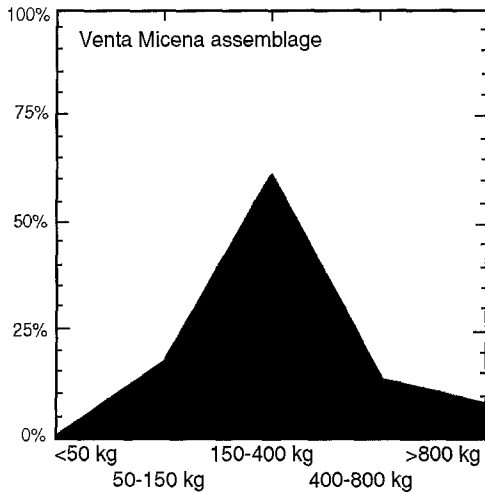


FIGURE 31 - Mean percentages of several ungulate size classes (a: <50 kg, b: 50-150 kg, c: 150-400 kg, d: 400-800 kg, e: >800 kg) in Venta Micena. *Pourcentage des moyennes des classes de taille de plusieurs ongulés (a: < 50 kg, b: 50-150 kg, c: 150-400 kg, d: 400-800 kg, e > 800 kg) à Venta Micena.*

ce between both graphs is in the abundance of small ungulates (<50 kg), which are practically absent from Venta Micena. This may be explained if we consider that these carcasses were almost entirely consumed on the spot where the large extinct hyaenas found them, rather than being carried back to their dens. A similar selective behavior has been reported among modern spotted hyaenas (Brain 1981; Kruuk 1972).

If hyaenas failed to transport the carcasses of individuals of small species to their dens, this preservational bias could then explain the scarcity of ungulate prey of very small size, which are represented in the fossil assemblage by only one distal epiphysis of a metacarpal of Caprini gen. et sp. indet. (a species weighing between 8 and 10 kg). Such selective behavior in the transport to dens of carcasses by hyaenas could then lead to poorer preservation of the young of small species in the assemblage than the juveniles of large species, thus affecting the interpretation of differential size effects on hunting success proposed here. However, this bias is only important for species of less than 50 kg, since those ungulate species weighing 50-150 kg (*Hemitragus alba* and Cervidae gen. et sp. indet.) are well represented in the Venta Micena collection (MNI = 14 and 20, respectively), in a proportion similar to that found among ungulates scavenged by spotted hyaenas (Fig. 30). Consequently, the increasing value of the juvenile/adult ratios as a function of body size for ungulate species weighing more than 50 kg (Fig. 25) is not an artefact of size effects on differential bone transport by hyaenas.

The results obtained clearly indicate that *P. brevirostris* was a bone-cracking scavenger in the Venta Micena palaeocommunity. It fed mainly on carcasses of animals killed and partially consumed by other flesh-eating carnivores, in contrast with the behaviour of modern spotted hyaenas, which are both hunters and scavengers (Kruuk 1972). The strong representation of juveniles among ungulate species identified at Venta Micena, 40.4% (80/198) of all individuals, suggests that the bone assemblage was an accumulation made by primary predators (Brain 1981; Shipman 1981; Vrba 1980). However, in primary assemblages most individuals tend to fall into a relatively restricted body size, according with the predator's preferences, and the carnivore/ungulate ratio is usually high, while at Venta Micena the body weight distribution of ungulate species is very wide (approximately 8-6000 kg: i.e., nearly three orders of magnitude) and the value of the carnivore/ungulate ratio is rather low, only 14.1% (28/198), what indicates that the bone assemblage was predominantly a non-primary, scavenged one. These data support the previous conclusion that the Venta Micena hyaena was specialized in scavenging ungulate prey hunted selectively by other carnivores.

With respect to very large ungulate prey species identified at Venta Micena (>1000 kg), *H. latidens* was probably the only such carnivore species capable of hunting them, since only modern lions and spotted hyaenas can hunt juveniles or critically ill individuals of such large species. So far as other ungulates are concerned, one of the most suitable candidates for predation seems to be the canid *C. falconeri*, as suggested by the high frequency of osteopathologies. These canids must have pursued their prey over long distances, like modern African wild dogs, thus leading to intense selection of individuals unable to withstand prolonged running. This hypothesis is supported by the finding of numerous juveniles of ungulate species of intermediate size (46% horse, 42% large deer, and 60% buffalo), since lions and spotted hyaenas do not select young individuals among modern ungulate species of comparable sizes (Table 3) as strongly as they are represented in the Venta Micena assemblage.

The high proportion of juveniles of larger species (elephant and hippo) in the assemblage indicates that the hunting behaviour of the saber-toothed felid *H. latidens* was similar to that of the modern African lion. The proboscidean *M. meridionalis* is represented in the fossil assemblage by five individuals, four of which are juveniles. The worn molars of the remaining individual suggest that it was old and probably died of starvation, being subsequently scavenged by hyaenas. Similarly, a

study by Rwan-Schatzinger (1992) of the Friesenhahn Cave assemblage, which was accumulated by the great scimitar cat *Homotherium serum*, has revealed a very high selection (almost 100%) of juveniles among the two proboscidean species identified in this site (*Mammuthus americanus* and *Mammuthus cf. columbi*). In contrast, other ungulate species of smaller body size such as *Mylohyus nasutus*, *Odocoileus virginianus* and *Bison* sp. are represented in this assemblage by much lower percentages of young individuals (40%, 33% and 50%, respectively). As noted above, lions are only able to hunt very young elephants, because the large size of adults makes them virtually invulnerable to predation. The high selection of juveniles of large ungulate prey species in Venta Micena suggests then that the hunting behavior of large machairodonts would be similar to that of recent large felids, which first subdue prey with their claws while biting the neck, as opposed to specialization in the capture of large proboscideans by stabbing them with their elongated canines and waiting for the prey to bleed to death, as suggested in some classic studies. Otherwise, the proportion of adult individuals of large ungulate species in the assemblage would have been much higher.

With regard to the possible ecological role of *M. whitei* in this paleocommunity, we can offer some morphofunctional considerations which have been published elsewhere (Martínez-Navarro & Palmqvist 1995, 1996; Palmqvist et al. 1996a). The results of a comparative study of the skeletal remains of *M. whitei* suggest that the dimensions of this machairodont differ markedly depending on whether they are estimated from the teeth or from the postcranial skeleton. When body size is calculated with minimum squares regression analysis (Van Valkenburg 1990) of lower carnassial tooth (M_1) length on body weight in modern species of felids (i.e., the procedure followed in this work; see Table 1), the value obtained is of only 55 kg. This suggests that this African species was leopard-sized (Martínez-Navarro & Palmqvist 1995). On the other hand, surface area of the diaphyseal cross section of the humerus in this species is approximately half of that in *Homotherium*, thus suggesting a weight of at least 100 kg for *M. whitei*. However, the width of the distal epiphysis of the humerus, which articulates with the radius, is greater in *M. whitei* than in a leopard or even in the male lion, which would suggest that the animal was somewhat larger than this latter species (i.e., around 200 kg). Obviously, these three independent estimates differ widely, although the most reliable of them is probably that obtained from the diaphysis of the humerus, given that the section of this long bone bears the weight of the forepart of

the body. If we consider this estimate correct, we are then dealing with a predator of about 100 kg, whose muscular strength used in immobilizing prey (estimated from the width of the distal epiphysis of the humerus) while it used its elongated canines to kill was four-fold greater than would be suggested by its food requirements or the speed at which it could eat (deduced from its markedly reduced carnassials). We therefore have a hypercarnivorous felid which would presumably generate large amounts of carrion, since it would exploit the carcasses of its prey to a small degree, thus leaving enough meat and all within bone nutrients for the large hyaena *P. brevirostris* and for the hominids. In the light of this likely situation, the recent discoveries of evidence on human presence both at Southern Spain and Georgia associated with African *M. whitei* (Martínez-Navarro & Palmqvist 1995, 1996) are not surprising, since this latter species would have made the first dispersal of hominids to Eurasia in the lower Pleistocene possible, due to the greater scavenging opportunities it provided.

Figure 25 shows the direct relationship between the abundance of juvenile individuals of those ungulate species preserved in the Venta Micena assemblage and the weight estimated for the adults; however, there are two distinct trends in this graph: the proportion of young increases gradually from 14.3% in *H. alba* to 59.3% in Bovini cf. *Dmanisibos*, decreases to 33.3% in *Stephanorhinus etruscus*, and increases again from the latter species to 80.0% in *Mammuthus meridionalis*. According with the above discussion, the first group of species (< 1000 kg) were presumably hunted by *M. whitei* and *C. falconeri*, while those of the second one (> 1000 kg) were probably predated by the large scimitar cat *H. latidens*. Figure 32 shows the results of separate regression analyses in both groups of species. The statistical fit obtained for the first set of ungulates ($r = 0.967$, $p = 0.002$) is better than that obtained for all species in the former analysis ($r = 0.841$, $p = 0.004$), which tends to strengthen the assumption of differences in the optimum prey-size for these carnivores.

CONCLUSIONS

- The macrovertebrate assemblage of Venta Micena presents an accumulated taphonomic stage and is constituted by demic and autochthonous palaeobiological entities recorded in situ (sensu Fernández-López 1991). This bone assemblage shows the highest diversity of large mammals recovered from any Plio-Pleistocene lacustrine site in the Guadix-Baza basin. The density of bones is very high, their orientation shows a random pattern, and more than 90% of the skeletal

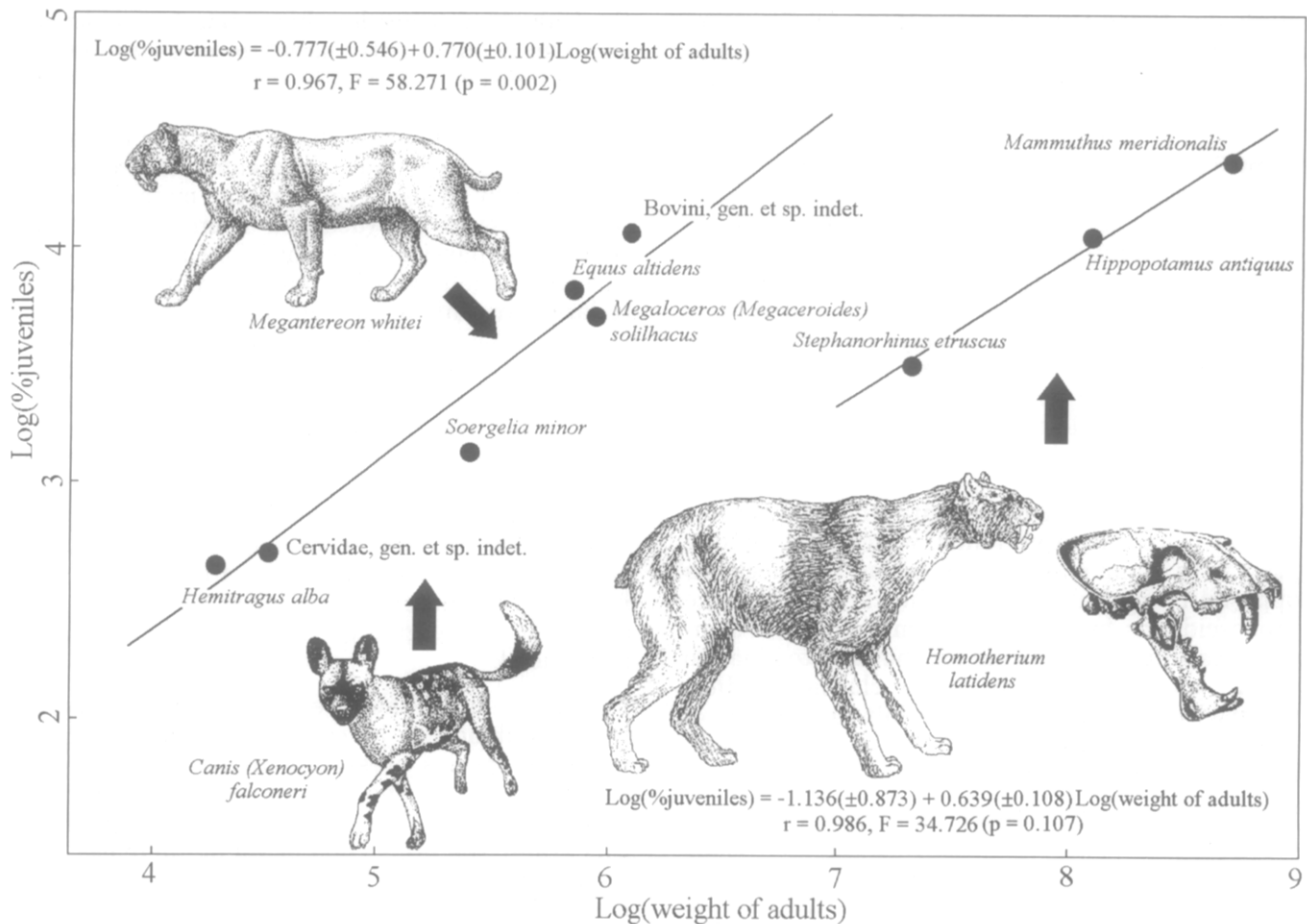


FIGURE 32 - Results of separate regression analyses of the abundance of juvenile individuals on mean adult weight for two groups of ungulate species from the Venta Micena assemblage, the first of which (< 1000 kg) were presumably hunted by *Megantereon whitei* and *Canis (Xenocyon) falconeri*, and the second one (> 1000 kg) by *Homotherium latidens*. Reconstruction of *Megantereon* from Antón (1996); reconstruction of *Homotherium* from Martin (1989). *Résultats d'analyses de régression séparées de l'abondance des individus juvéniles sur le poids moyen adulte pour deux groupes d'espèces d'ongulés de l'assemblage de Venta Micena, le premier d'entre eux (< 1 000 kg) était probablement chassé par Megantereon whitei et Canis (Xenocyon) falconeri et le second (> 1 000 kg) par Homotherium latidens. Reconstitution de Megantereon d'après Antón (1996); reconstitution d'Homotherium d'après Martin (1989).*

elements are in contact with others. The surface of the bones was exposed to the effects of subaerial weathering for a very short time in most cases (0-1 years). The bones are not dispersed horizontally, since 20% of them are articulated and the remaining 80% are found associated. Biostratigraphic fractures, gnawing marks and coprolites are very abundant. Differential fragmentation of major long bones by hyaenas is suggested by the close relationship between the abundance of epiphyses and complete elements, and their structural density and marrow content, respectively.

- Quantitative analysis of size/abundance patterns of ungulate species at Venta Micena indicates that the preservational bias produced during the taphonomic history of this assemblage affected predominantly species of smaller body

size. Once the original abundance of each species is estimated, the size/abundance relationship shows a good fit to the predictions of Damuth's model for a fossil assemblage formed by attritional mortality. The preservational characteristics of the bones from this fossil assemblage and the results of a multivariate comparison of the relative abundance of postcranial bones in assemblages from hyaena, leopard and porcupine lairs, as well as carnivore open feeding grounds and bone accumulations made by the man, suggest that the Venta Micena assemblage was formed by the accumulation of skeletal remains near the entries of shallow dens dug by hyaenas near the ponds that surrounded the Orce lake. The use of descriptive and quantitative taphonomic analyses for the study of Venta Micena allows to propound a general model for the characterization of fossil

assemblages generated by the activity of hyaenids, for which this palaeontological site is probably the best example of the collecting-modifying behaviour of *Pachyrocata brevirostris*.

- Interspecific analysis of the proportion of juvenile individuals among ungulates in relation to the body weights estimated for adults indicates a strong selection of prey by carnivores. This selection is corroborated by the finding of many bones with different osteopathologies such as arthrosis, which limited the locomotive capabilities of the animals and therefore their ability to escape predation. The sex ratio of large bovids and equids, which is highly biased in favour of females, also points to this hypothesis of prey selection, as females are more vulnerable to predation given their smaller body size. These results thus fully confirm that the Venta Micena assemblage was formed by attritional mortality produced by carnivores on the ungulate populations, and allow us to rule out that the assemblage originated from catastrophic mortality events.

- Comparison of the relative frequencies at which ungulates of different sizes are killed and scavenged by the main African predators, and the proportions in which different sized ungulates are found in the Venta Micena assemblage, suggests that hyaenas there fed largely on carcasses of animals hunted by the large machairodont *H. latidens* and by the hypercarnivorous canid *C. falconeri*. Morphofunctional analysis of the medium-sized saber-tooth *M. whitei* shows that it may have also played a significant ecological role in this palaeocommunity as a source of ungulate carcasses for both hyaenas and hominids.

Acknowledgments - This research was supported by a general grant from the "L.S.B. Leakey Foundation" and by a Spanish governmental major research grant, Projects PB94-1222-CO2-02 and PB97-1082, from the "Dirección General de Investigación Científica y Técnica". Professor María Teresa Alberdi allowed us to make the geochemical analyses in the laboratory of "Museo Nacional de Ciencias Naturales" of Madrid. We gratefully acknowledge to Professor Jordi Martinell (University of Barcelona) his encouragement to write this article for *Geobios*, to Mr. Mauricio Antón (Museo Nacional de Ciencias Naturales, Madrid) his permission to use his drawings of *Pachyrocata* and *Megantereon*, to Dr. Bienvenido Martínez-Navarro (Museo de Paleontología de Orce, Granada) and to Dr. Alain Turq (Musée National de Préhistoire, Les Eyzies de Tayac) their helpful comments. And, last but not least, we want to express our acknowledgment to Professor Claude Guérin (Université de Lyon) and Professor Richard A. Reymont (University of Uppsala) their constructive review of the original manuscript. This is contribution number 10 of the "Orce Research Project".

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A. ARRIBAS

Museo Geominero
 Instituto Tecnológico Geominero de España (ITGE)
 Ríos Rosas, 23
 E-28003 Madrid

P. PALMQVIST

Departamento de Geología y Ecología
 (Área de Paleontología)
 Facultad de Ciencias, Universidad de Málaga
 E-29071 Málaga
 E-mail: Paul.Palmqvist@uma.es.